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THE UNIVERSITY OF ALBERTA

EFFECTS OF ANT ATTENDENCE ON APHIDS

by

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University of Alberta

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled EFFECTS OF ANT ATTENDENCE ON APHIDS submitted by C.L.GRIFFITHS in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

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Abstract

The mutualistic relationship between two species of aphids, *Aphis varians* Patch and *Aphis neogillettei* Palmer, and the ant, *Formica fusca* (L.) was examined. It was determined that the ants confer several benefits on the aphids. Tended aphids survived better than untended aphids. This was attributed to a reduction in stress caused by interruptions in feeding. Ants demonstrated an ability to reduce predation and parasitism. A number of physiological affects were found - decreased alatae production at low densities, increased growth and fecundity, and increased rate of maturation. The hypothesis that these affects are caused by the exogenous application of a junvenile hormone analogue found in the saliva of *F. fusca* was made. The potential for competition between the aphid species for tending ants was discussed.

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1. Introduction

The object of this thesis was to examine the potential for competition between 2 species of aphids for the services of a common mutualist: ants. To accomplish this objective, it was first necessary to examine the mutualistic relationship itself. For the purposes of this thesis symbiosis shall be defined as the prolonged and intimate relationship over evolutionary time of organisms belonging to different species. Mutualism shall be used in the context of a symbiotic relationship that is mutually beneficial to the organisms involved. It may be either facultative or obligate.

Competition for limited resources over evolutionary time has often been cited as an important selective force in species differences and community organization (Price, 1975). However, it has been suggested that competition among insect species may be unimportant because of the biological features of insects suggesting r-selection (Pianka, 1970). Wiens (1977) has also disputed this ubiquitous role for competition in variable environments.

Recent insect studies have not produced a clear answer regarding the evolutionary significance of competition in insects (Heatwole and Davis, 1965; Clench, 1967; Istock, 1973; Dybas and Lloyd, 1974; Benke and Benke, 1975; Denno and Cothran, 1975; Heinrich, 1976; Young, 1972; Shapiro, 1974; Rathcke, 1976).

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Mutualism has been investigated only recently in regards to its ecological and evolutionary role (Goh, 1979). Mutualistic relationships are many and varied in nature, but until the last few years have not been considered from the viewpoint of community structure and dynamics (May, 1973, 1976; Rescigno and Richardson, 1973; Albrecht et al, 1974; Hirch and Smale, 1974; Christiansen and Fenchel, 1977; Goh, 1979; Vandermeer and Bouche, 1978). Despite these beginnings, mutualism is still a very poorly understood interaction and the discrepancy between the theoretical predictions and the growing volume of evidence on mutualism is striking. Essentially, theory predicts that mutualism should only be common in the tropics (i.e., in a relatively constant environment)(Vance, 1978; May, 1976), and relatively less common than predator-prey and competition interactions (Goh, 1979). This is because mathematical theory says that mutualistic relationships represent a destabilizing force in ecological communities. Yet mutualism is present and reasonably widespread in the temperate zone and has been demonstrated to be an important force in the structure of some communities.

The mutualistic relationship investigated in this research is the relationship between ants and aphids. Ant-homopteran relationships have been described in the literature since the late nineteenth century. Nixon (1951) surveyed the literature on the mutualistic relationship between homopterans and ants and concluded that the

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beneficial effects of ant attendance for aphids were largely overstated and that the benefits were confined to "accidental" protection from predators and better hygiene from the removal of accumulated honeydew. Fourteen years later Way (1963) reviewed the then recent research and came to a very different conclusion. He detailed the structural modifications of ant-attended aphid species, demonstrated the delaying effect on alate production, modification of life cycle, active protection from predators, benefits from living within ant nests and "shelters", increased rate of growth, feeding, excretion and larviposition, sanitiation, and transportation of aphids. The importance of honeydew as a food source for species of ants that show tending behavior was implied. The evidence presented strongly supported the hypothesis of a mutualism (non-obligatory for most species) that exerts significant influence on population structure and dynamics. Since that time very little research has been conducted on the ant-aphid relationship. The work that has been done has been mainly directed toward the effect of ants on alatae production and their use in biological control.

Addicott (1978a, 1978b, 1978c, 1979) has described a multispecies aphid-ant association on *Epilobium angustifolium* L. (fireweed) in Colorado. He demonstrated that tending by ants was beneficial to three of the four aphid species present and that this effect was density-dependent. It was also shown that some ant species were more effective than others in increasing aphid colony

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survival. Analysis also suggested that one species, *Aphis varians* Patch, was not as successful when its colonies were located near woody plants with tended aphids. Addicott (1978b) hypothesized that this was the result of competition between the aphid species for tending ants. As a result of that study the present research was initiated to examine the mutualistic relationship between an ant species, *Formica fusca* (L.) and two aphid species, *A. varians* and *Aphis neogillettei* Palmer, and to determine if the potential for competition between the aphid species for tending ants existed. Because of technical field difficulties that developed during the course of the study, the hypothesis of competition was not tested experimentally.

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2. Life Histories

2.1 *Aphis varians*

The phenology of *Aphis varians* was first thoroughly described by Patch(1927). She found *Aphis varians* to be a dioecious aphid that overwinters (diapauses) as an egg on *Ribes spp.* (currants). The fundatrix matures sometime in late May and produces apterae (wingless parthenogenic females). The second generation apterae mature and reproduce on currant bushes, their large colonies often causing severe damage to the leaves and new shoots. The third generation, produced throughout June, is a mixture of apterae and alatae (winged parthenogenetic females). The alatae leave the currant plants for fireweed, the summer hosts, where they establish themselves on the buds and tips of the rapidly growing inflorescences. For the rest of the summer mature viviparae produce apterae and alatae on the fireweed. The alatae may disperse to new plants. In late summer and fall the alate females leave the senescing fireweed and return to the currant bushes, where they produce oviparous females. Alate males, that are produced on the fireweed, migrate to the currant bushes where they mate with the oviparae. The overwintering eggs are then deposited on the currant bushes (see Figure 1 for summary).

Aphis varians is tended by several species of ant. In the central Alberta region, *F. fusca*, *F. neorufibarbis* Emery, *F. sanguinea subnuda* Emery and *Camponotus herculeanus*

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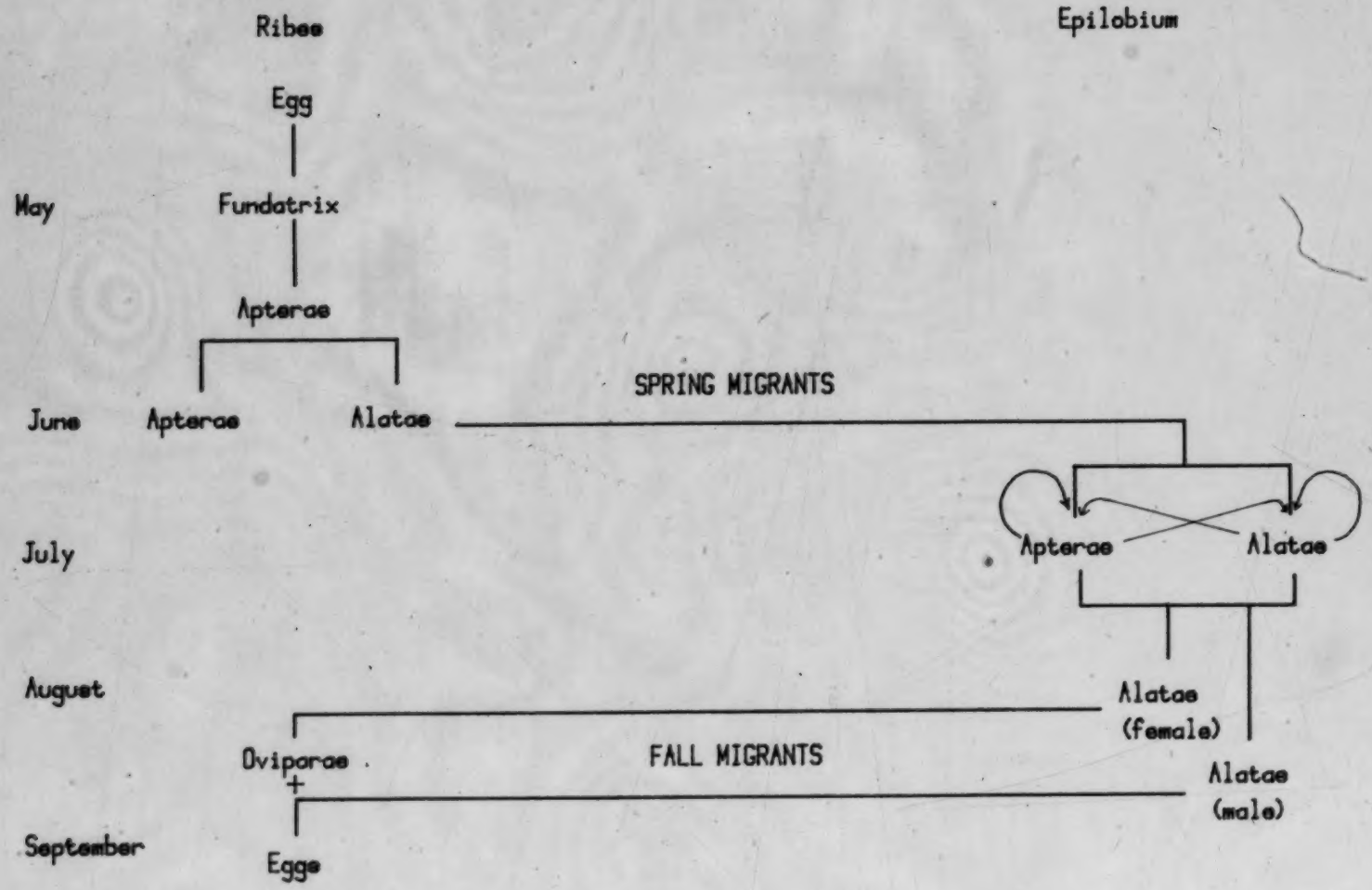
Figure 1. Life Cycle of *Aphis varians*.



(L.) have been found tending *A. varians*. Addicott (1979) listed ten ant species including *F. fusca* that tended *A. varians* in Colorado.

2.2 *Aphis neogillettei*

The life history of *A. neogillettei* can be inferred from Palmer (1952), Robinson and Chen (1969) and field observations made over the course of the present study.

Aphis neogillettei is a monoecious aphid whose entire life cycle occurs on *Cornus stolonifera* Michx.(dogwood). The fundatrix matures in mid-May and produces apterae. The apterae then mature and begin reproducing on the rapidly developing flower terminals. From this time viviparae produce both apterous and alate viviparae, depending on local conditions. Apterous viviparae were observed moving between flower terminals on the same plant, and it is assumed the alatae may disperse to new plants. In mid-June large, dense colonies could be found on the inflorescences. These colonies were usually tended (94%, n=270, Edmonton, Alberta). By late June, early July the colonies migrate to the new leaves on growing shoots. This is probably a response to the declining nutrition of the fruit/flower terminals where the fruit has begun to ripen. The aphids cause extreme curling of the leaves. At this time, the aphids enter a "summering" state during which growth and reproduction are slow, alates are rarely produced and few new colonies are initiated. The number of colonies as well

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as their density seemed to decline over the summer. Most colonies were tended. Those that were not were covered in honeydew and the plants had sooty mold growing on them.

In late August sexuals develop. From August 15-17, of 419 colonies (leaves with aphids) observed, 293 contained males. Mating occurs, and the overwintering eggs are laid on dogwood in the space between the leaf buds and twigs throughout September (see Figure 2 for summary).

In central Alberta *F. fusca*, *F. sanguinea subnuda* and *Tapinoma sessile* (Say) have been found tending *A. neogillettei*.

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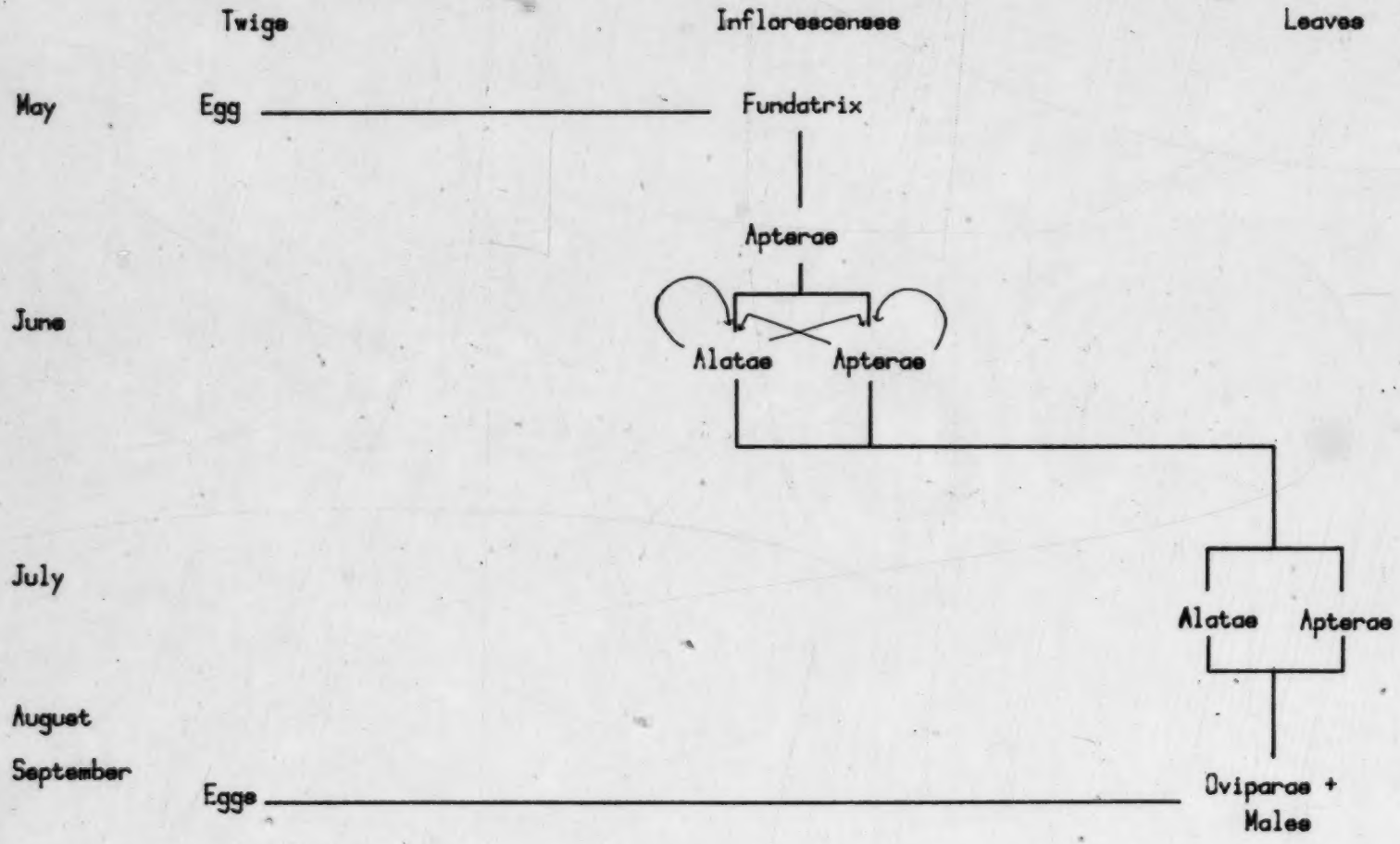
2.3 *Formica fusca*

Formica fusca is a small formicine ant with a comparatively unsophisticated foraging behavior (Wallis, 1964). Nests are usually small with many vertical shafts and occasionally are covered with a thatched mound (Sudd, 1967). Populations within nests are low, often with fewer than 200 workers (Wallis, 1964). However, *F. fusca* will form multi-queen colonies with large population numbers.

In a series of papers Wallis (1961, 1962a, 1962b, 1962c, 1962d, 1964) described the foraging behavior of *F. fusca*. Activity was determined in great part by temperature and wind (Pickles, 1935; Ayre, 1958). Pickles (1935) found *F. fusca* did not become active until ground temperature reached 10°C. Wind prevented activity.

Figure 2. Life Cycle of *Aphis neogillettei* on *Cornus stolonifera*



Formica fusca forage singly. Well defined trails are not made. However, Moglich and Holldobler (1975) found that *F. fusca* does secrete a chemical from the hindgut which is laid on the ground from a food source to the nest. This chemical serves as an orientation cue, but only ants stimulated by a returning forager respond to it. Foraging is restricted to a relatively small area surrounding the nest (maximum 26 feet - Pickles, 1935).

Early food studies suggest that honeydew is the major food item in the diet of *F. fusca* (Pickles, 1935).

The following observations were made during the course of the present study. *Formica fusca* were found foraging on the buds and closed inflorescences of woody plants as early as May 4, 1977 (Lesser Slave Lake, Alberta). At this time little insect prey is available and little, if any, honeydew. The earliest aphid colonies were found on the buds and closed inflorescences of woody plants such as white spruce and poplar. By May 14, 1977, *F. fusca* was observed tending small colonies of *A. neogillettei* on dogwood flowers. Thus, it would appear that the early foraging on inflorescences and buds of woody plants insures the early discovery of aphid colonies. Ayre(1959) found that *F. subnitens* Creighton would switch from feeding on plant sap to honeydew as soon as aphids became available.

From early May until the last week of September, 1978, a minimum of 4 and an average of 10 *F. fusca* colonies were examined in the Edmonton area every 2 weeks. Qualitative

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observations were made regarding the presence and relative abundance of eggs, larvae, pupae and winged sexuals. On May 7 eggs were found in all nests, but no larvae were located. Larvae were first located on May 14 and they increased in frequency until early July. Pupae first appeared between May 25 and May 30. Pupae continued to be present until August 16. On June 29 winged sexuals were found in 3 of 4 nests. Sexuals continued to be present until July 19. At this time there were few larvae in any of the nests examined, however many pupae were still present. No larvae were found by mid-August. By September no brood was found in any nest examined (see Figure 3 for summary).

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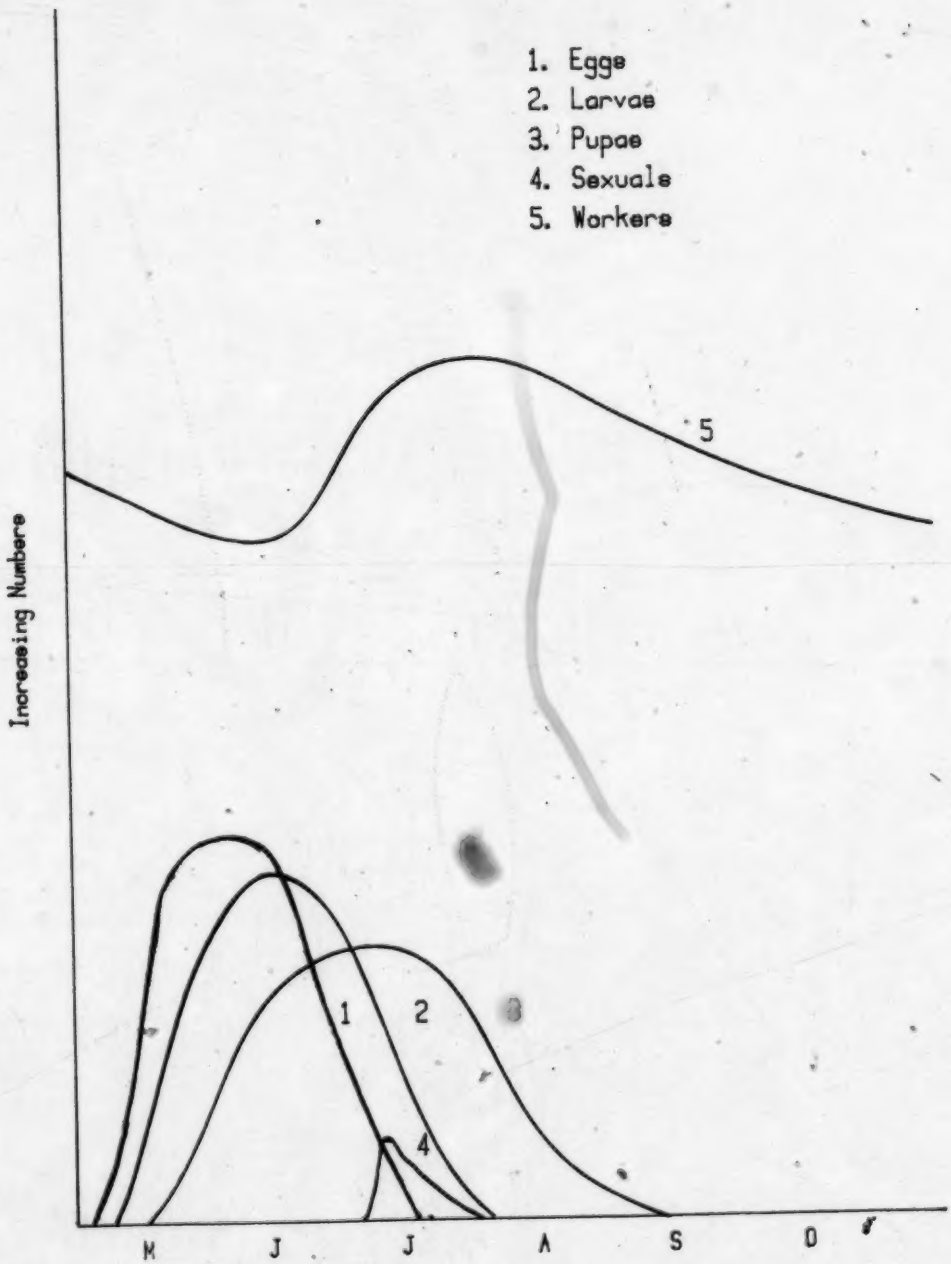

Figure 3. General phenology of *Formica fusca* from qualitative observations.

3. Ant Experiments

3.1 Objectives

The overall objective of this study was to determine if tending by *F. fusca* had a beneficial effect on *A. varians* and *A. neogillettei*, and if so, did competition occur between these aphid species for attendant ants. However, before experiments could be conducted on these problems a number of preliminary experiments were conducted so that certain variables could be controlled. Experiments were designed to determine if the queen was requisite to foraging activity, what density of ants would be sufficient for tending, and what effect varying aphid densities had on tending behavior. Once the preliminary questions had been answered a final experiment was undertaken to answer the questions posed by the overall objective.

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3.2 The effect of the queen on foraging activity

3.2.1 Methods

Experimental field plots were established in an open field at the University of Alberta Experimental Farm at Ellerslie. Plastic lawn edging (15.25 cm in width) was used to enclose thirty 2 x 2 m plots. The plots were rendered ant-proof by a band of Tree Tanglefoot (Tanglefoot Company, Grand Rapids, Michigan) smeared on the lawn edging. A large dogwood shrub was planted in each plot in early May and thirty fireweed plants from the growth chamber (see section

4.2.1) were transplanted into each plot in early June.

Ants were collected for the experiment in late May in the following manner. A large sheet of canvas was spread on the ground next to a nest of *F. fusca*. The nest was then shovelled onto the canvas sheet and the ants were hand sorted until the queen was located. The queen was placed in a screw-top 1 quart jar with a specially modified lid. The lid was modified such that the center section was covered with fine nylon mesh. Three holes were drilled near the edge of the lid that would permit passage of the workers while restricting movement of the queen because of her larger body size. The holes were blocked with masking tape until the start of the experiment. Nest material was placed in the nest-jar. Three hundred workers and as many larvae and pupae as possible were collected and placed in the nest-jar with the queen.

A total of six colonies were collected. Three colonies contained queens and three were without queens. The colonies were kept in the lab for one week and then placed in six of the experimental plots at Ellerslie. The nest-jars were located in holes in the ground so that their lids were level with the surface in order to help maintain a lower temperature within the nest-jar. The tape was removed from the lids and the ants were allowed to forage. The number of ants foraging in each plot was recorded every 18 minutes from 9 am to 5 pm for 5 days by observing each of the plots consecutively for 2 minutes and counting all ants observed

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outside of the nest-jar. An ant was considered to be foraging if it was exhibiting exploratory behavior at a distance of 15 cm or more from the nest-jar. There were no aphids, artificial food sources or fireweed present. The dogwood was still blooming, however.

3.2.2 Results and Discussion

A Friedman's test was conducted on the data collected from each colony to determine if the number of ants foraging changed over the day. The Friedman's test is a distribution-free test analogous to the two-way analysis of variance without an interaction term, or more specifically, a one-way analysis of variance with blocking. As only 1 replication per treatment was available from this experiment, no interaction was assumed. The first hour and a half of each day consistently had the lowest values. If this time period was deleted from the data no difference could be detected in the numbers foraging from 10:30 am to 5 pm ($.50<p<.70$) (Figure 4). The median number of foraging ants on a daily basis ranged from 1% to 3% of the total number of ants in the nest-jar. This is quite low compared to the results obtained by Ayre (1962).

A Friedman's test was used to determine if the presence of a queen affected the median number of ants foraging each day. Because there was greater than 1 replication per block in this experiment, a test for significant interaction was conducted before the Friedman's analysis (Mehra and Sen,

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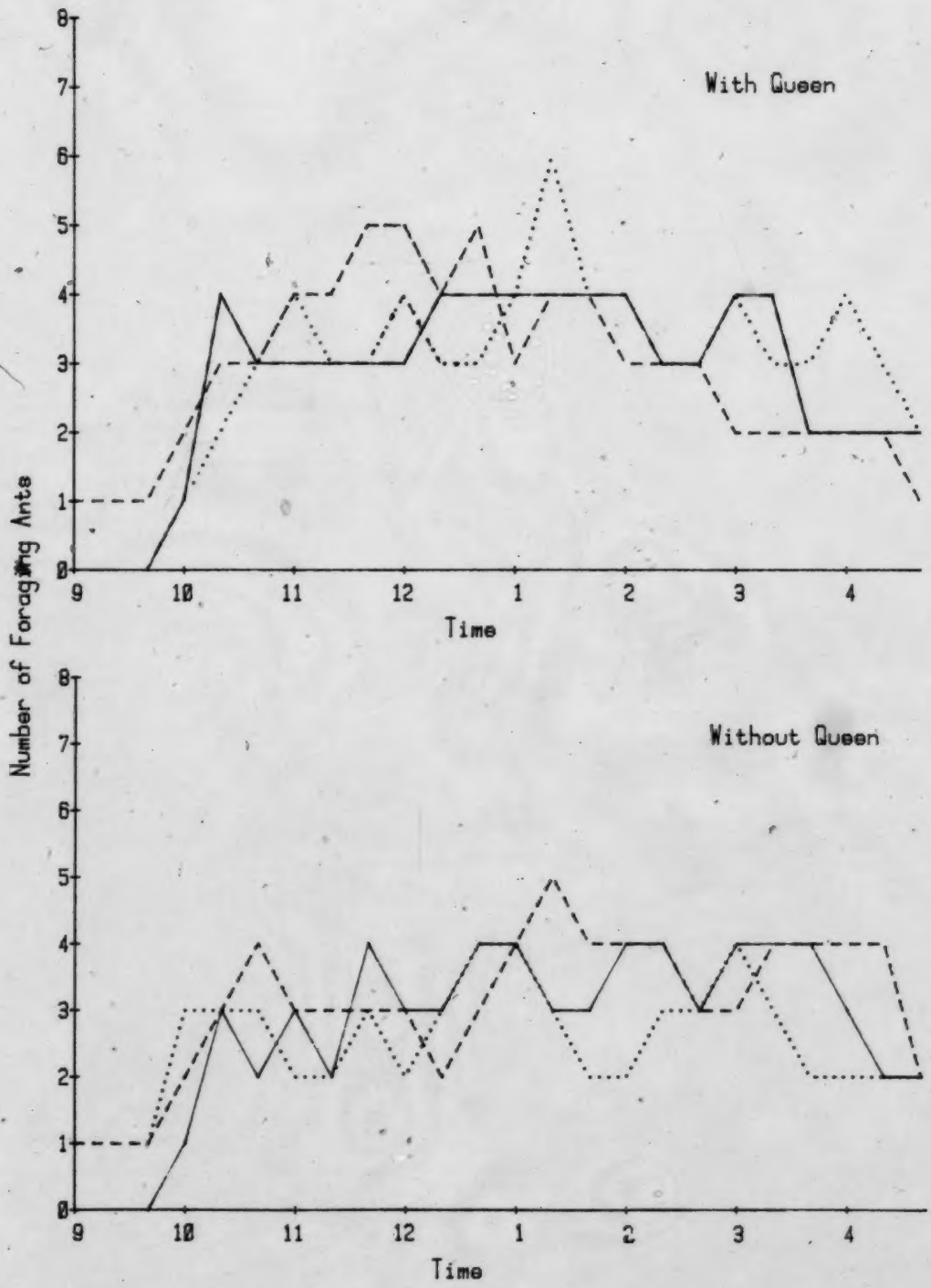

Figure 4. Median number of foraging ants for days 1 to 5 at 20 minute intervals from 9 a.m. to 5 p.m. for colonies with and without queens.

1969). As the Friedman's test assumes no interaction it is important where possible to test for interaction. No significant interaction was found in this data. No significant difference ($p=.49$) was found in the numbers foraging from colonies with and without queens (Table 1). However, a significant decreasing trend was found in the numbers foraging from day 1 to day 5 ($p<.001$)(Table 1).

This experiment implied that, for a given day, the number of foraging ants did not change from mid-morning to evening, and that the presence of a queen did not affect foraging activity. These results indicated that it was not necessary to collect queen ants (a time consuming task) for future experiments. It also showed that twice daily counts of the number of foraging workers would provide an accurate account of the foraging activity for a given day. Foraging numbers did decrease significantly from day 1 to day 5. This cannot be explained except perhaps the lack of food in the plots discouraged foraging activity.

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3.3 Foraging activity at sugar baits

3.3.1 Methods

This experiment was designed to determine the size of ant colony that was required to provide adequate tending of the aphid colonies. Adequate tending was defined for this experiment as having 1 ant per aphid colony. Each ant colony was also expected to tend 30 aphid colonies. This level of tending was assumed to be adequate for future experiments

Table 1. Median number of ants foraging per day from colonies with and without queen.

Day	With queen	Without queen	Median
1	4.5	5.5	5.00[1]
2	3.5	2.5	3.00[2]
3	2.5	2.5	2.50[3]
4	2.5	2.5	2.50[3]
5	3.0	2.0	2.50[3]
Median	3.00[1]*	2.5[1]	

*Values superscripted by the same number are not statistically different within the same row or within the same column.

Source	Friedman's X^2	df	probability
Queen	.467	1	.49
Time	131.455	4	<.001

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since aphid colony size would be small (3 - 6 adult aphids). Sugar baits were used to simulate aphids.

Queenless colonies were collected for these experiments by using a wood dowel (5 cm in diameter - 60 cm in length) to disturb nests of *F. fusca*. As the ants attacked and crawled along the dowel, they were counted and shaken into a bucket whose interior had been sprayed with Fluon (Tygadure). Fluon is a Teflon metal-mould releasing agent which makes smooth surfaces extremely slippery. When sprayed on the walls of plastic buckets it has the effect of making them unclimbable by ants.

The ants were then transferred to a nest-jar along with any larvae and pupae that could be found. Three nest-jars containing 1000 workers each and three nest-jars containing 1500 workers each were collected and placed in plots at Ellerslie as before (see section 3.2.1). Densities of 300 from the previous experiments had proven too low, as at least 30 tending ants were required and 3% of the total worker population was the maximum obtained (i.e., 9 out of 300). Hence, a minimum of 1000 workers was set. From previous field collecting it was observed that nests of over 1500 workers were uncommon. Fifteen hundred workers was set as a maximum colony size for this experiment, as very large nests (nests with more than 1 queen) were only periodically located.

Sugar baits consisting of two 5 ml pipettes filled with 3% and 20% sugar water coloured with red food colouring were

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placed in each plot equal distance from the ant colony. The tops of pipettes were plugged with modelling clay to prevent the sugar water from leaking. The concentration of 20% sugar was chosen as it falls within the range of sugar concentrations found in honeydew which varies from 10% to 27% sugar content (Maltais and Auclair, 1952; Lamb, 1959). The 3% concentration was used to determine if ants discriminate sugar "quality".

The number of ants feeding at each pipette was recorded every five minutes from 9 am to 4 pm for 5 days. Initially, the ants were observed from sunrise to sunset, but as no ants were observed foraging before 8 am or after 7 pm, and few before 9 am and after 4:30 pm the 9 am to 4 pm schedule was adopted.

Behavioral observations were made on individual ants, recording the length of time spent feeding at a sugar bait, whether or not the ant returned directly to the nest, and if so, by what path.

A sugar bait was also located 1 m from a natural *F. fusca* nest near the Ellerslie test site. The behavior of individual ants at three 5 ml pipettes filled with 20% sugar solution was recorded. The ants were timed while feeding and their movements afterwards were monitored until it was determined that they were returning to the nest.

3.3.2 Results and Discussion

A Friedman's analysis was conducted to determine if

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ants selected one sugar solution over the other. The daily total number of ants foraging at each of the concentrations for each nest was considered a block. At neither density was there a significant difference between the numbers of ants foraging at the two sugar concentrations (Tables 2 and 3). The numbers of ants feeding at the sugar baits on the first day from 4 of the 6 nest-jars greatly exceeded (20 times as great) the numbers feeding on the four subsequent days. The range of the percentage of workers feeding (excluding the first day) was 0% - 1.1% at density 1000 and 0% - .007% at density 1500. The percentage of workers foraging, when compared to those feeding at the sugar baits, was considerably higher; 1.4% - 3.6% at 1000 and .8% -3.13% at 1500. The majority of these ants were foraging on the fireweed, presumably for nectar as no aphids were present.

Friedman's analysis detected no significant difference in the total numbers foraging at the sugar baits, expressed as a percent of the total worker population, between the two densities (Table 4).

The time spent feeding at the sugar baits was analysed with a two-way analysis of variance (Table 5). The factors were sugar concentration and whether or not the ants returned directly to the nest after feeding. The interaction was not significant ($p=.10$), nor was the concentration of the sugar solution ($p=.96$). However, the ants that returned directly to the nest-jar fed for a significantly longer time than those that did not ($p<.01$).

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Table 2. Total number of ants per day feeding at sugar baits at 3% and 20% sugar concentration from colonies at density 1000.

Colony	Day	Sugar Concentration 3%	20%
1	1	70	77
	2	3	2
	3	4	4
	4	3	8
	5	5	6
2	1	2	6
	2	0	0
	3	1	0
	4	1	0
	5	2	1
3	1	47	40
	2	0	3
	3	2	3
	4	4	2
	5	2	2
Median		2^{1}*	2^{1}

*Values superscripted by the same number are not statistically different.

Source	Friedman's X^2	df	probability
Concentration	.27	1	.60

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Table 3. Total number of ants per day feeding at sugar baits at 3% and 20% sugar concentration from colonies at density 1500.

Colony	Day	Sugar Concentration 3%	20%
1	1	12	13
	2	2	1
	3	4	1
	4	0	2
	5	2	1
2	1	95	112
	2	1	0
	3	2	2
	4	1	1
	5	3	0
3	1	45	30
	2	5	4
	3	3	8
	4	2	4
	5	3	2
Median		3^{1*}	2^{1}

*Values superscripted by the same number are not statistically different.

Source	Friedman's X^2	df	probability
Concentration	.60	1	.44

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Table 4. Percent of total workers in each colony foraging at sugar baits.

Day	Density 1000	1500
1	14.7	1.7
	.8	13.8
	8.7	4.9
2	.5	.2
	.0	.1
	.3	.6
3	.8	.3
	.1	.3
	.5	.7
4	1.1	1.3
	.1	1.3
	.6	4.0
5	1.1	.2
	.3	.2
	.4	.3
Median	.5[1]*	.6[1]

*Values superscripted by the same number are not statistically different.

Source	Friedman's X^2	df	probability
Density	1.152	1	.28

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Table 5. Average time (in seconds) spent feeding at sugar baits for ants that did or did not return to the nest after feeding.

Concentration	3%	20%	Average
Returned	122 (n=17)	106 (n=20)	114[1]
Did not return	66 (n=11)	81 (n=19)	73[2]
Average	94[1]*+	93[1]	

*Values superscripted by the same number are not statistically different within the same row or within the same column.
+Differences in factor level means were determined by Scheffe multiple contrast procedures.

Anova Table

Source	SS	df	MS	F	prob.
Returned	26755.68	1	26755.68	11.423	<.01
Concentration	5.27	1	5.27	.002	.96
Interaction	6414.69	1	6414.69	2.739	.10
Error	147569.66	63	2342.38		
Total	180745.31	66			

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In the field plots 37 ants returned directly to the nest after feeding while 30 did not. Most of these continued to forage on the fireweed. In contrast to this, 51 ants were observed under natural conditions and all but 2 returned directly to the nest. The average time spent feeding by ants from the wild nest was 78±43.9 sec (n=51). This time was not significantly different from the time of the captive ants feeding on 20% baits ($t=1.707$, $df=88$, $p<.90$). The ants from the nest observed under natural conditions travelled more or less directly to and from the baits from the nest along the same trail. This implies that the ants feeding at the bait were being recruited from the nest rather than from other foragers. Individuals were observed to cross this trail and ignore it even when very near the bait. However, if they met an engorged ant on the trail they immediatedly travelled to the bait.

The objective of this experiment was to determine an adequate number of ants for tending. A minimum of 30 ants feeding at the sugar baits was defined as "adequate". This minimum was achieved by 2 of the 3 nest-jars at each ant density on the first day. From the results of this experiment, it was decided that 1000 workers would be adequate for the aphid tending experiments. However, after the first day the numbers feeding at the sugar baits dropped dramatically. This same feeding pattern has been demonstrated by Wallis (1962d). He showed that satiation of recipient ants (refusal of proferred food) within the colony

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halted the activity of primary foragers of *F. fusca*. A second possible explanation of the result in the present study is the inadequacy of the sugar bait as a food source. Throughout the experiment many workers foraged on the fireweed rather than on the sugar baits. Half the workers that fed at the sugar baits did not return to the nest, but continued to forage on the fireweed. These ants spent significantly less time feeding on the sugar solution than those that returned to the nest. Plant sap and exudates, as well as honeydew, contain substantial quantities of amino acids, in addition to carbohydrates. Although these sources have never been shown to be a complete diet for an ant colony in that successful rearing of larvae and egg production cannot be sustained, healthy colonies of adults can be kept for relatively long periods on such diets (Lamb, 1959). The sugar baits possibly provided a good carbohydrate source, but may not have been sufficiently attractive (in competition with fireweed) to maintain ant interest.

This experiment also suggested that the ants did not discriminate between the 2 concentrations of sugar water. I think this is a valid reflection of an inability to determine the quality of a food "type". This does not contradict the above results which imply an ability to discriminate between food "types" (e.g., a carbohydrate source vs a protein source).

An assumption implicit in the decision to use densities of 1000 ants for the aphid experiment was that the numbers

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tending would not decline as they had when the ants were feeding at the sugar baits. There are two arguments in support of this assumption. The first involves the adequacy of honeydew as a food source as compared to a sugar solution. The second is that those ants that returned to the nest-jar after feeding were replete (i.e., their gasters were greatly extended). The ants would require a longer period of time to become replete when feeding on honeydew. This would lead to the maintainance of higher tending numbers.

3.4 Effect of varying aphid densities on ant tending behavior

3.4.1 Methods

A .6 x .6 m plot was delineated with 4 cm masking tape on a laboratory bench. The tape was smeared with Tree Tanglefoot, making the enclosure ant-proof. A nest-jar of 300 workers, an undetermined number of larvae and pupae, but no queen, was placed in the plot. Cat food and water were supplied to the colony but no sugar source was provided. This was to encourage the ants to tend the aphids. Six aphid colonies consisting of apterous adult *A. varians* on potted fireweed (see sec 4.2.1) were placed in the plot after one week. The six colonies were divided into 2 groups (group I and group II) and placed at opposite ends of the plot equi-distant from the nest-jar. The densities of aphids chosen were based on information about natural *A. varians*

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colony densities (see section 4.2.3). Each of these groups was composed of three aphid colonies with low, medium and high aphid densities (low; 10-15, medium; 50-60, high; >100). The number of ants tending each colony was recorded every hour from 8 am to 5 pm for ten consecutive days. Individual ants were dabbed with water soluble paint as they climbed onto a plant. The length of time each ant spent tending was recorded. It was noted if the same ant returned to tend again in a given day. This could not be determined reliably as the ants periodically groomed the paint off their abdomens and off the abdomens of other ants.

After 10 days 3 more plants (group III), one with each density of aphids, were introduced and the number of tending ants recorded hourly for five more days. At the end of the experiment the aphid colonies were to be collected to determine densities. An accidental fumigation of the stock cultures necessitated maintaining these individuals for future stock. Hence, this experiment was not repeated and no exact measures of the aphid densities could be made.

3.4.2 Results and Discussion

Over the first 10 days of the experiment the total number of ants tending did not change (Cox-Stuart test for trend, Marascuilo and McSweeney, 1977, pp. 66). Group I aphids were very poorly tended relative to the group II aphids (Table 6). The difference in the degree of tending was investigated by a Wilcoxon matched sample test and was

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Table 6. Median number of ants per day tending *Aphis varians* colonies at high, medium and low densities.

Density	Group	Median for days 1-10	11-15
High	I	2.5^{1*}	0.0^{1}
	II	8.5^{2}	9.0^{2}
	III	-	7.0^{12}
Medium	I	0.0	0.0^{1}
	II	4.0	4.0^{2}
	III	-	3.0^{12}
Low	I	3.0^{1}	0.0^{1}
	II	2.0^{1}	1.0^{1}
	III	-	1.0^{1}

*Values superscripted by the same number are not statistically different within the same column within the same density group.

Wilcoxon two-sample test for differences between group I and group II for days 1 to 10

Density	T	probability
High	-3.836	<.001
Medium	N/A	
Low	-0.549	.583

Kruskal-Wallis test for difference between groups I, II and III for days 11 to 15.

Density	H	df	probability
High	13.035	2	.001
Medium	10.707	2	.005
Low	4.562	2	.102

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found to be significant at the medium and high density, but not at the low density. An accumulation of honeydew occurred on the group I medium and high density colonies, which suggests that a lack of honeydew was not the reason for poor attendance.

On day 11 after the introduction of the 3 new aphid colonies the ants completely abandoned the group I aphids. The total number of ants tending increased significantly with the additional ants tending the group III aphids (Cox-Stuart test for trend, Marascuilo and McSweeney, 1977, pp. 66). However, group II aphids were still tended by significantly more ants than group III aphids (Kruskal-Wallis test, Table 6), but no honeydew accumulation was observed on any group III colony. Therefore, it can be assumed that tending levels were adequate.

The range of the percent of workers tending the aphids in this laboratory experiment was 4.7% to 10.3% of the total worker population, which is within the range of the numbers foraging in a field colony (Ayre, 1962).

The average time spent tending was 337±43 min (n=17). The tending time for field ants was not obtained during this study and is not noted in the aphid literature. A comparison of the two potentially could have served as a measure of the honeydew quantity/quality produced by the aphids on the potted fireweed.

Formica fusca workers sustained a higher level of activity when honeydew was the food source compared to sugar

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solutions or fireweed. Although the two groups (I and II) were not tended equally, the total number of tending ants did not change over the first 10 days. The introduction of a third group of aphids increased the numbers tending, however, suggesting that the "desirability" of the aphid colonies determined the numbers tending. The factors determining "desirability" are not known at this time. The plants were chosen for uniformity of size and state, and the aphids were randomly chosen from the stock cultures. However plant "quality" (indirectly honeydew quality and quantity) could be determined by a number of uncontrolled factors. Therefore, additional experimentation is required to clarify this factor.

As final population counts could not be made on the aphid populations, it was not possible to estimate the aphid to ant ratio for each colony. As such no conclusion could be drawn regarding differences in numbers of ants tending aphid colonies at different densities.

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4. Aphid experiments

4.1 Objectives

A series of experiments were designed to determine if tending by *F. fusca* affected life history and population parameters of *A. varians* and *A. neogillettei*. The parameters were number of aphids surviving after a specific time period, maturation rate, number of alatae produced, total body length and fecundity. Protection from predators and parasites for *A. varians* was also examined.

4.2 Methods

4.2.1 Stock Cultures of *Epilobium angustifolium*, *Aphis varians* and *Aphis neogillettei*

Epilobium angustifolium seed was collected in the late summer of 1977 from three large, vigorous fireweed plants growing on the same rootstock at Lesser Slave Lake, Alberta. The seed was stored over the winter in brown paper bags at 5°C. In late April 1978 germination tests indicated 40-60% germination. At this time seeds were germinated in 5 cm square peat pots (1080 pots) in standard potting soil mixture. The pots were maintained in a growth chamber controlled at 20°C, 65-80% relative humidity, 1500 footcandles light and 14/10 LD regime. The germinating seeds were covered with plastic to maintain high humidity. When sprouts reached the hook stage, they were thinned to one per pot. The plants were watered daily and fertilized once per

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week with C.I.L. 20-20-20 Plant Treat (1 tblsp/gal). In late May a second group of 1080 plants were seeded. When the young plants reached a size of 15 cm some were transferred to 15 cm azalea pots, while 900 were planted in the plots at the Experimental Farm (30 per plot).

A Hansen Weatherport portable greenhouse (2.75 x 4.5 m) was erected in an open field at the Experimental Farm adjacent to the plots. Two large dogwood shrubs were planted inside the greenhouse. Environmental conditions were not controlled in the greenhouse. Temperatures inside the greenhouse ranged from 3 to 32°C. Light levels in the greenhouse were approximately 80% of exterior light.

In late May colonies of *A. neogillettei* were collected from the wild by placing infected inflorescences in a vial and bringing the entire colony to the laboratory. After inspection for predators, parasites and other aphid species, the infected inflorescences were tied to the inflorescences of the dogwood shrubs in the greenhouse. After 48 hours most of the aphids had moved onto the shrubs and the old inflorescences were removed. The colonies were allowed to disperse naturally.

Colonies of *A. varians* were collected in late June in the same manner as *A. neogillettei*. Fifty potted fireweed plants located in the growth chamber were infected using the same technique as for the dogwood. Fifty additional fireweed plants were planted in the greenhouse and infected. By mid-July it was necessary to wash excess honeydew from some

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of the colonies to prevent fungal growth by placing the plant under a gentle stream of flowing water.

4.2.2 Experiments With *Aphis neogillettei*

Six experimental plots (45 x 60 cm) were delineated on lab benches by 4 cm masking tape. The tape was smeared with Tree Tanglefoot. A nest-jar colony of 300 workers of *Formica fusca* was placed in each plot. The ants were collected by the method described in section 3.2.1. For one week prior to the experiment the ants were fed on cat food and water, but were not given any sugar.

Thirty-six uniform-sized leaf cuttings were made from new leaf terminals of dogwood shrubs. These were placed in vials of water. The leaf cuttings were randomly divided into three groups of twelve, and each group assigned to a density treatment of 10, 50 or 100 *A. neogillettei*. These densities were chosen to match the densities to be used for *A. varians* in future experiments. The appropriate number of adult apterous aphids from the stock cultures maintained in the greenhouse were transferred to the cuttings. If an aphid was feeding it was necessary to disturb the aphid by gently pushing on the head until it removed its stylets from the leaf. The aphid was then picked up by a leg with fine forceps and placed on a leaf surface of the cutting. After 24 hours all progeny were removed. After an additional 48 hours the adult aphids and excess (numbers greater than the desired density) first instar nymphs were removed. The

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cuttings within each density treatment were then randomly assigned to a tending treatment such that each of the six ant colonies had a colony of each density to tend. The 18 remaining control colonies were placed along the edges of the plots. Fluorescent Gro-lites and three 150 watt floodlights were used to illuminate the plots on a 16/8 LD regime. The temperature fluctuated between 20-23°C.

The number of ants tending each colony was recorded every 15 minutes from 8 am to 5 pm for the first 2 days and every hour from 8 am until 5 pm for the last 10 days of the experiment. The time between excretions was measured for a number of tended and untended aphids.

After 12 days the aphids were collected and stored in 90% alcohol. Before dissection and measuring the aphids were cleared in phenol/chloral hydrate (van Emden, 1972) and then transferred to lactic acid where they were stained with basic fuschin (Elliott, 1973). The aphids were measured and dissected under a Wild M-5 stereoscopic microscope (8x - 40x) equipped with an eyepiece micrometer.

The following information was recorded for each aphid:

1. Morph and instar

   No alates were found in the colonies. First and second instar larvae were classified together. They were significantly smaller than the other aphids, being the progeny of the original aphids that had matured. Third instar apterae are difficult to differentiate from fourth instar apterae and for *A. neogillettei* were

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classified together. Adult apterae are distinct from the juveniles.

2. Total body length

   Total body length was measured from the frontal tubercles to the anal plate ventrally.

3. Length of antennal segments

   The length of the third to sixth antennal segments was measured.

4. Embryos - length and number

   Embryos were dissected out, and counted. Total body length was measured. Staining made it possible to identify large embryos, but less well developed embryos could not be reliably seperated from abdominal structures. Large is used here to describe embryos with distinguishable eyespots, mouthparts and legs..

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4.2.3 Experiments with *Aphis varians*

Five of the six plots used in the *A. neogillettei* experiment were used in the *A. varians* experiment. The ant colonies were replaced with newly collected ant colonies of the same density that were sugar starved for 1 week prior to the experiment. Fireweed plants were selected for uniformity of inflorescence size from the plants grown from seed in the growth chamber. The plants were randomly divided into three groups and each group was assigned a density treatment of 10, 50 or 100 aphids. These densities were chosen to relate to natural populations. Addicott (1978c) found median population size never exceeded 100 aphids per fireweed shoot

during the summer and until mid-August did not exceed 50 aphids per shoot. Adult apterous aphids from the stock culture maintained in the growth chamber were randomly transferred to the plants at the appropriate densities in the same manner as *A. neogillettei* had been transferred. After 12 hours all progeny were removed. After an additional 12 hours all adults and excess progeny were removed. The plants within each density treatment were then randomly assigned to a tending treatment such that each ant colony had one aphid colony of each density to tend. The remaining control plants were placed at the edges of the plots. Fluorescent Gro-lites and three 150 watt floodlights were used to illuminate the plots on a 16/8 LD regime. The plants were watered daily. The temperature ranged from 20 to 24°C.

The number of ants tending each colony was recorded every 15 minutes for the first 24 hours, then every 15 minutes from 9 am to 5 pm the second day, and finally every hour from 8 am to 5 pm daily until the first progeny appeared on day 8.

The time between excretions was measured for a number of tended and untended aphids.

The aphids were collected by cutting the inflorescences and placing them in a vial of 90% alcohol. The aphids were then removed from the inflorescences under a stereoscopic dissecting microscope with a fine paint brush or fine forceps. In this manner no aphids were missed. They were then cleared, stained and measured in the same manner as *A.*

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neogillettei with the exception of the instar classification. It is possible to distinguish between first and second instars by the number of antennal segments, firsts having 4 and seconds having 5 (Patch, 1927). Alatae are distinguishable by third instar by the presence of wing pads. Fourth instar alatae have more developed wing pads to seperate them from thirds. The adults have wings as well as a different body shape (see Figure 5). The apterae pose a greater problem. Again the adults are easily distinguished by general appearance. The second and third instars also appear different when seen together. However, there is overlap in the distribution of total body and antennal lengths. Therefore, the instars were classified based on appearance (see Figure 6). The frequencies of different body/antennal length combinations were then plotted (Figure 7). Overlap was found only in a central area between the extremes and lends support to the use of general appearance as a method of classification. Both instars had only 5 antennal segments, although a few third instars had 6. Third instar apterae were separated from fourth instars by the number of antennal segments (thirds with 5, fourths with 6) and by general appearance.

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4.2.4 Predation Experiment

Three plots similar to the plots in the laboratory were constructed on a piece of plywood in the greenhouse at Ellerslie. *Formica fusca* colonies of 300 workers were placed

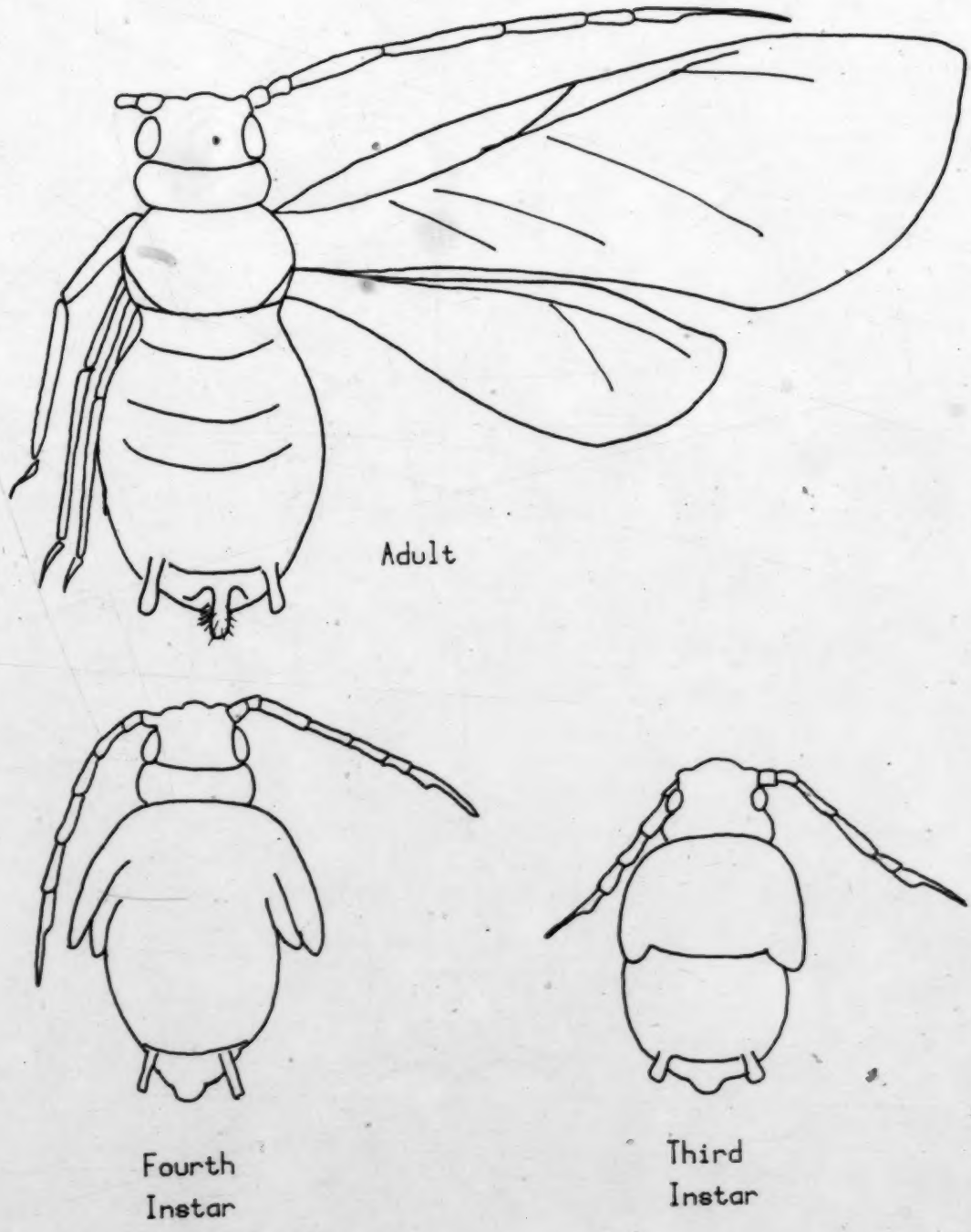

Figure 5. Alate morph of *Aphis varians*.

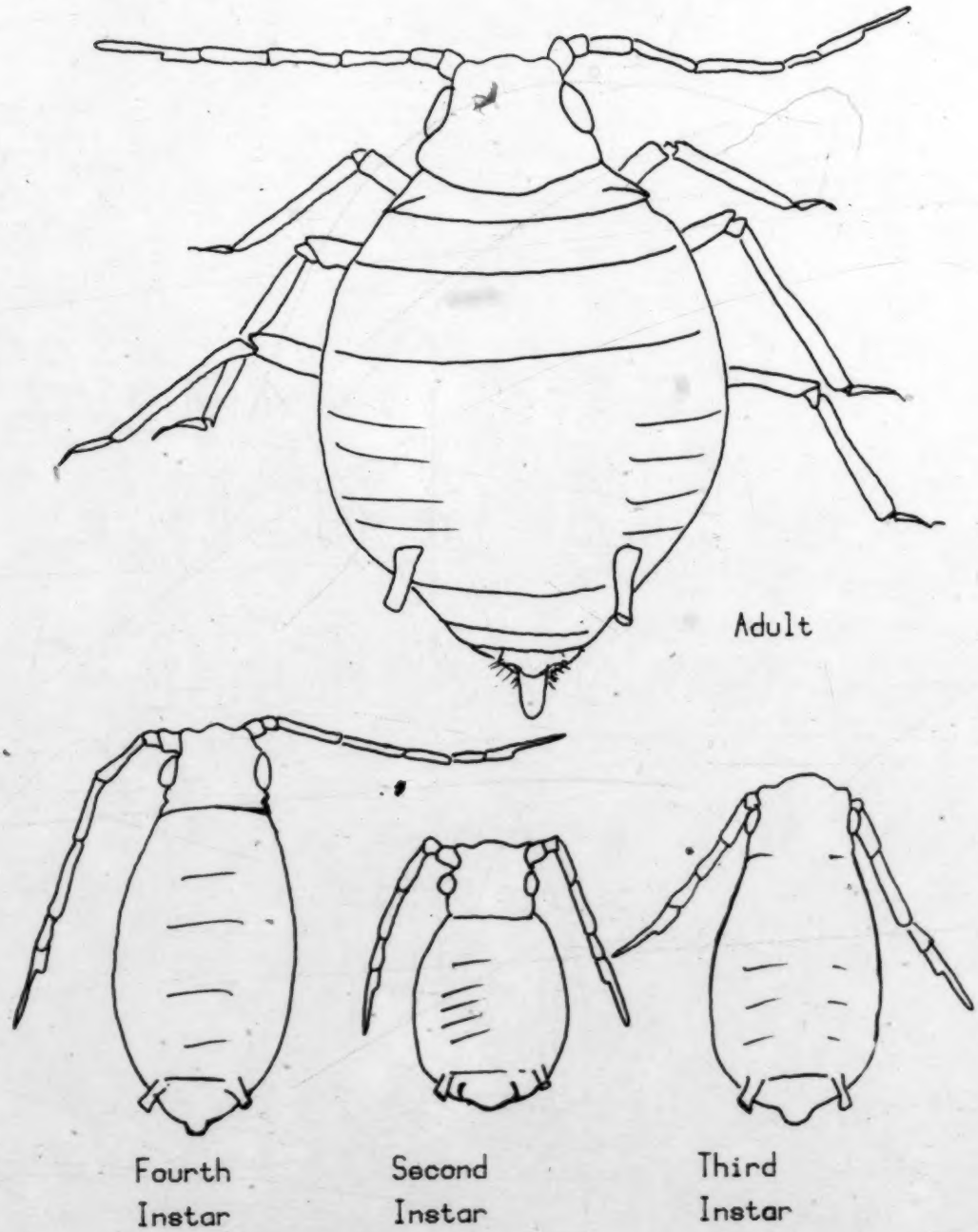

Figure 6. Apterous morph of *Aphis varians*.

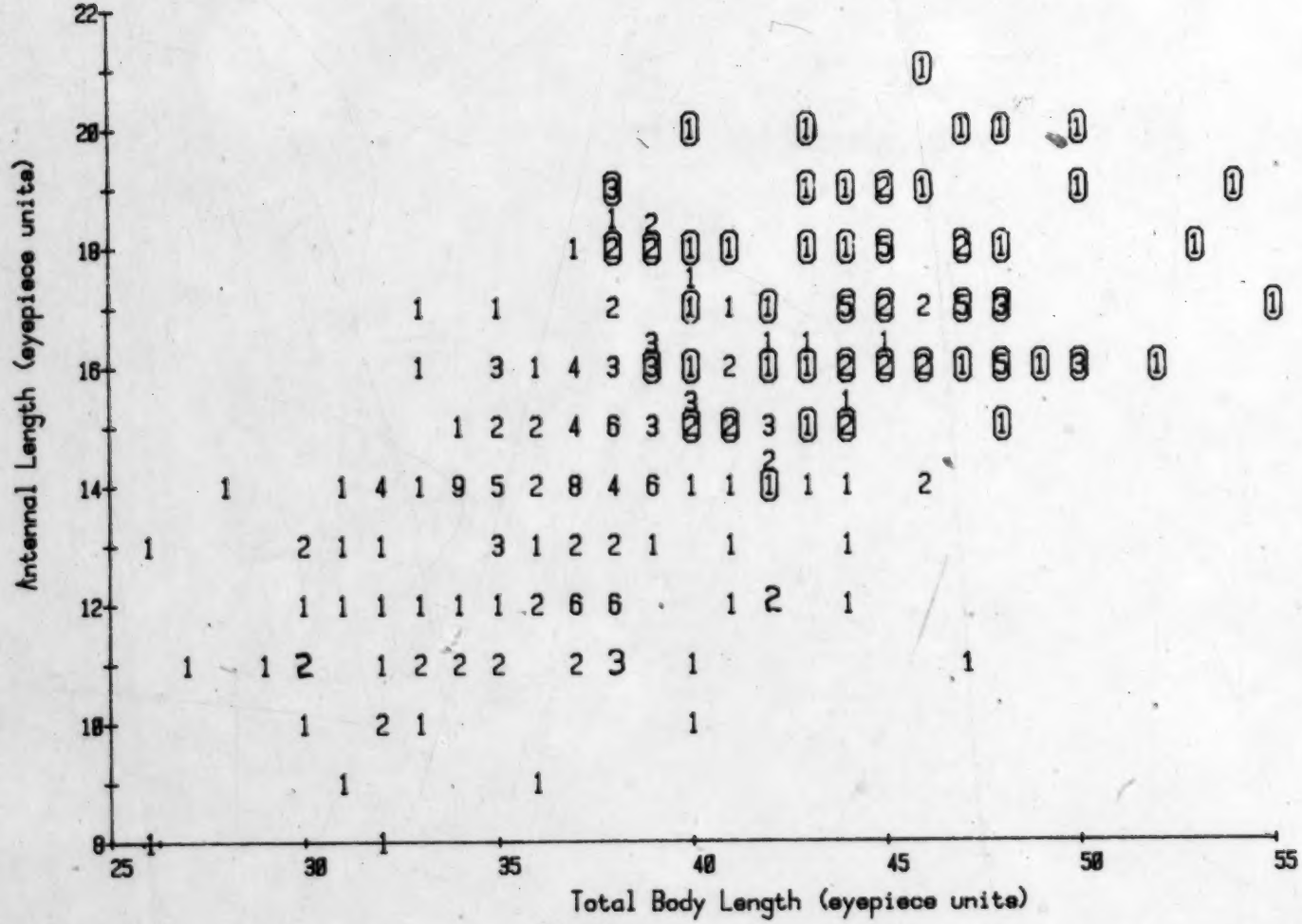

Figure 7. *Aphis varians*: Frequency of antennal vs total body lengths of second and third instars. (1 eyepiece unit = .0239mm) (Third instars circled.)

in two of the plots and the third was left empty as a control. Five potted fireweed infected with 15 apterous adult *Aphis varians* were placed in each of the plots containing an ant colony and 10 infected plants in the empty plot.

Every morning for 2 weeks the colonies were observed from 9 am to 10 am. The plants were watered daily and the ants fed cat food and water. It was noted if a colony was tended and if any predators were present.

4.3 Results and Discussion

4.3.1 Plant Growth

Fireweed plants in the greenhouse and field plots grew vigorously attaining heights of 80 - 100 cm. The potted fireweed in the growth chamber did not grow as well. Maximum heights of 60 cm and an average nearer 40 cm were attained. Although these plants were smaller than those grown in the field they did not appear to be unhealthy, nor were they sparsely foliated. All the plants bloomed producing inflorescences from 10 to 20 cm in length. In appearance and size they greatly resembled the small mountain willow-herb, *Epilobium latifolium* L.. Fireweed grown from seed do not attain the size of plants starting from rootstocks (Myerscough and Whitehead, 1966). Light levels down to 43% daylight have little effect on fireweed growth, but fireweed is highly suseptible to nutrient stringency, particularly phosphates and nitrates (Myerscough and Whitehead, 1967). In

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particular, plants grown from seeds require a tremendous commitment of nutrients to growth to reach reproductive size. Fireweed grown from rootstocks in 15 cm azalea pots with the same fertilizing regime the previous summer were tall and vigorous. It is therefore postulated that the stunted growth of potted plants in the present experiment was due to nutrient deficiency. However, the stunted growth should not have affected the overall experimental results since only uniform sized plants were used in test situations.

4.3.2 Statistical Analysis

Two-way analysis of variance was used to detect significant factor effects in the data collected from *A. varians* colonies. Colony averages were used as replications within a treatment. As there was a question of dependence arising from the experimental design - each ant colony tended 3 aphid colonies - the error terms were examined for auto-correlation (Durbin-Watson test) and dependence (by plotting). No dependency effects were found. Data that were not normal and homoscedastic were transformed. If the interaction was significant, it was examined. If deemed important, treatment means were examined for differences using Scheffe multiple contrasts at 5% significance levels. Otherwise, factor level means were examined using Scheffe multiple contrasts at 5% significance levels.

Because a great many *A. neogillettei* colonies did not

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survive, at least one treatment had only 1 replication. Therefore, two-way analysis of variance with an interaction term could not be used. It was proposed to conduct a two-way analysis of variance with one replication per treatment, using the average of the colonies in a given treatment as the replicate. This analysis assumes no interaction between factors. The Tukey test for additivity was used to test this hypothesis and the means were plotted (Figures 8, 9, 10, 11). In all cases important interactions were apparent. Hence, data could not be examined for statistical significance, and conclusions drawn in the text are merely inferences from the graphs.

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4.3.3 Effect of Ant Tending on Predation

All aphid colonies in plots containing ants were tended in the greenhouse. A significantly greater proportion of the tended colonies vs untended colonies survived in the greenhouse after 2 weeks (9/10 vs 4/10; Fisher Exact Test, p=.054). At least 4 of the untended colonies were observed being preyed upon by adult coccinellids, while coccinellids were never observed on tended colonies. No parasitized aphids were found in the tended colonies, but 0-9% of the individuals were parasitized in the untended colonies with 2 of the 4 surviving colonies parasitized.

El-Ziady and Kennedy (1956) used exclusion experiments in field and glasshouse to determine the effects of *Lasius niger* (L.) on *Aphis fabae* Scopoli. They demonstrated that

the ants afforded the aphids some protection, but whether or not predators were present, *L. niger* increased the rate of aphid multiplication, and the protection was probably of secondary importance. Flanders (1951) showed that ants are important protectors of many aphid species. Herzig (1937 - cited by Way 1963) thought ants to have only a slight effect through protection when compared to their effects through stimulation of the aphids' reproduction. Banks (1962) demonstrated unequivocally that *L. niger*, a small, not especially hostile or predacious ant, was capable of completely protecting *A. fabae* from coccinellid, anthocorid, syrphid and chrysopid adults and larvae. However, ant attendence increased the predation by the wasp *Diaeretus sp.*. Banks also indicated that coccinellid, syrphid and chrysopid eggs were removed from the plants by attendant ants. The experiments conducted by Banks were of short duration and at low densities and may not be applicable in the field situation. To extrapolate to the field situation more information is needed regarding the impact of predators not only on a given colony, but on the entire population of an area, at what densities predators are effective and at what densities ants can confer sufficient protection. The evidence put forward by Banks (1962) and Banks and Macauley (1967) implies that ants are significant protectors only when aphid colonies are small.

The parameters of importance in assessing the significance of ant attendance on predator impact are:

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1. density of aphids
2. density of predators and their "hunting" ability
3. density of ants and their "protective" ability
4. microclimate (temperature and humidity)
5. long term tending patterns of ants
6. critical times for predatory limitation
7. overall predation rates for all colonies.

Rarely have these parameters all been measured. In a quantitative study using Hollings "component analysis" model Frazer and Gilbert (1976) concluded that no steady-state between predator and prey could occur (for coccinellid-pea aphid relationship), but that the field relationship was extremely resilient. The model predicted that any chance increase in the aphid numbers would allow aphids to gain and the beetles could not thereafter restore the balance. Conversely, the slightest decrease in aphid numbers would allow the coccinellids to drive the aphids to extinction. In the field however, the coccinellids left an exploited population before the aphids became extinct. Similarly, if the aphids overpopulated an area they dispersed because of population pressure.

Although there is sufficient evidence demonstrating that ants have the ability to protect aphids from predation and parasitism (Way, 1963; Hagen and van den Bosch, 1968; Stary, 1966), there is no information regarding the impact of this predation on the population of an area. There is no evidence that this protection significantly increases the

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fitness of the aphids either.

4.3.4 Physiological Effects of Tending

Ant attendance significantly increased the proportion of *A. neogillettei* colonies that survived in the laboratory ($p<.02$, Table 7). The percentage of original aphids that survived ranged from 16 - 80% for tended aphids and 24 - 50% for untended (see Figure 8). The graph clearly indicates an interaction caused by the single value from the untended density 50 treatment. The standard errors overlap almost completely suggesting no differences between the treatments.

All the *A. varians* colonies survived. The two-way analysis of variance on the data of the percent of original aphids surviving detected no interaction ($p=.772$) or density ($p=.945$) effects, but did suggest a difference between tended and untended colonies ($p=.089$, Table 8). In 3 colonies there was greater than 100% survival. In removing the adults and excess exules at the beginning of the experiment, it was only possible to insure that a minimum were left. The exules are very small and are sometimes not observed if they are under a bud etc. Only by examining the plants thoroughly under a microscope could all the exules have been found. This was considered to be too great a disturbance. Hence, more than the minimum densities may have been present. Addicott (1978c) found the average production of *A. varians* to be approximately 3 exules per day. As the adults had only 12 hours to reproduce, a maximum of 1.5

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Table 7. Number of colonies of *Aphis neogillettei* surviving after 12 days.

Density	Tended	Untended	Total
10	3	2	5
50	4	1	5
100	5	2	7
Total	12	5	

X^2 goodness-of-fit test.

	Tended	Untended
Survived	12	5
Died	6	13

$X^2 = 5.46$, df = 1, $p < .02$

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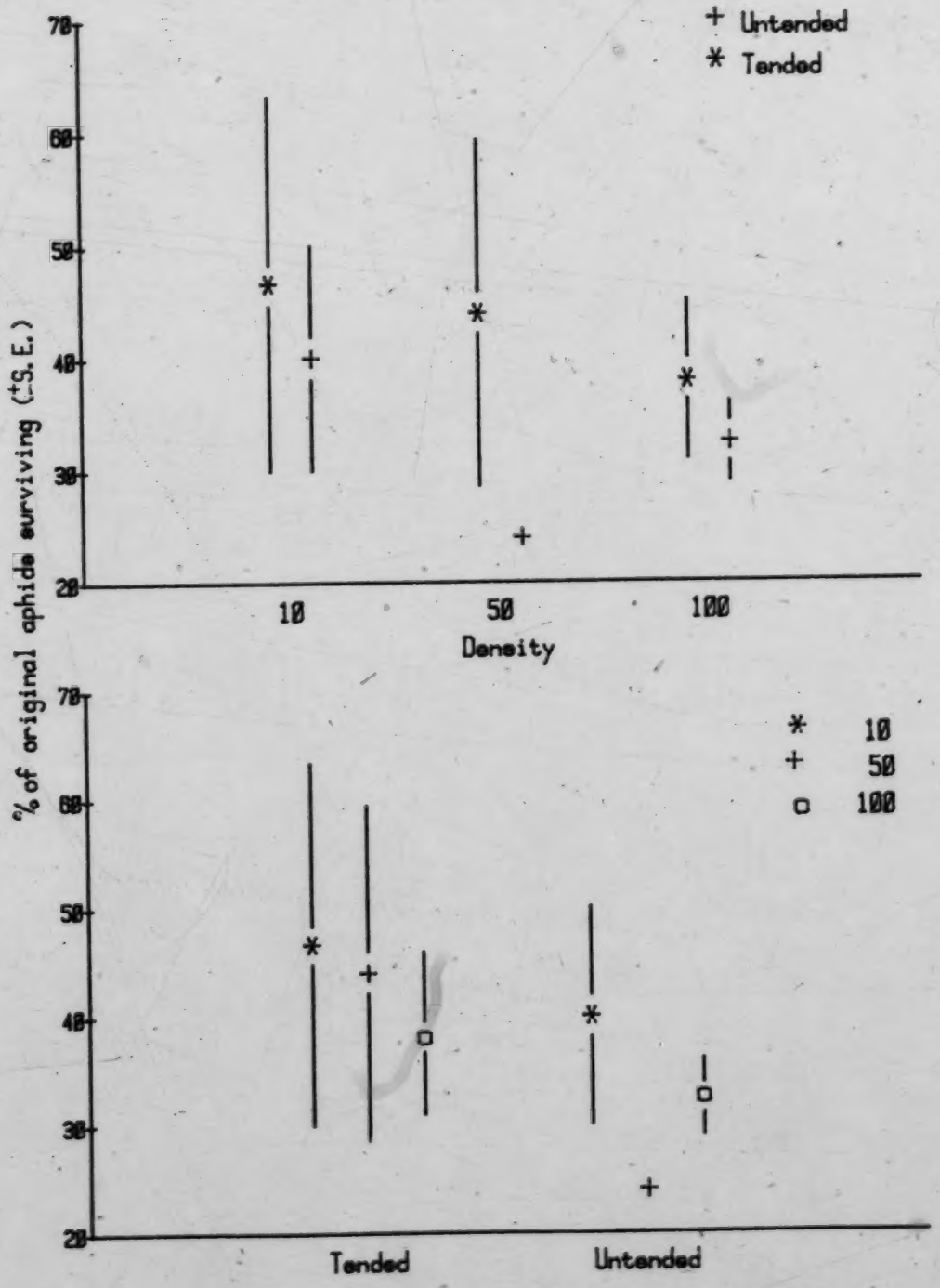

Figure 8. *Aphis neogillettei*: percent of the aphids that were originally placed on the *Cornus* leaves that were alive at the end of the experiment.

Table 8. Percent of original aphids surviving at the end of of the experiment for *Aphis varians*. (Data transformed 2 arcsin p for analysis.)

Density	Tended	Untended	Average
10	97.5	89.2	94.1[1]
50	98.1	91.5	95.3[1]
100	95.5	92.9	94.3[1]
Average	97.1[1]*+	91.3[2]	

*Values superscripted by the same number are not statistically different within the same row or within the same column.
+Differences between factor level means were determined by Scheffe multiple contrast procedures.

Anova Table

Source	SS	df	MS	F	probability
Tending	.5057	1	.5057	3.127	.089
Density	.0184	2	.0092	.060	.945
Interaction	.0846	2	.0423	.260	.772
Error	3.8811	24	.1617		
Total	4.4898	29			

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times the required number of exules was assumed. Many were removed so the excess was minimized.

Bradley and Hinks (1968) destroyed nests of *F. obscuripes* Forel and *Dolichoderus taschenbergi* (Mayr) near jack pine where colonies of several aphid species were being tended. The result was the disappearance of the aphid colonies. This experiment was begun in mid-June. In that research, as well as in other examples of obligatory mutualism, lack of protection from predation and parasitism have been cited as the cause of the aphid declines. These claims are often substantiated quantitatively (see Nixon, 1951). In the present experiment no predators or parasites were present. Hence, they could not be the cause of the significant decrease in survival of the untended *A. neogillettei* colonies or the slight decrease observed for *A. varians*. It has been shown in the literature that aphids become noticeably restless, moving about in and near the colonies after the removal of tending ants. In the present experiment untended individual *A. neogillettei* were observed walking down the petiole of the leaf where they had been placed. In all 50 and 100 density colonies some individuals relocated on the other leaf or the terminal. This never occurred in the tended colonies. No noticeable restlessness occurred in any *A. varians* colonies.

Work by Dixon (1963, 1966) on sycamore aphids (*Drepanosiphum platanoides* (Schr.)) revealed the nutritive status of the host plant (sycamore) changed markedly over

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the season. During the spring when new foliage was being produced the soluble nitrogen content in the leaves was high. The high nitrogen content dropped as the leaves matured and remained fairly constant over the summer. Once the leaves began senescing the nitrogen present was translocated out of the leaves to the branches, raising the level of soluble nitrogen again. The density of aphids on a leaf was positively correlated with the soluble nitrogen content as was the weight of first instars and adults. The reproductive rate was depressed by the poorer nutritive status. As noted earlier (section 2.2), *A. neogillettei* colonies summering on leaves demonstrate a pattern of slowed growth, lower reproduction and lower densities similar to those demonstrated by Dixon. Since predation and parasitism did not cause the extinction of the *A. neogillettei* colonies, I postulate that aphids feeding on mature leaves suffer a severe nutrient deficiency. Any disturbances that interrupt feeding for a significant length of time result in the death of those individuals in the poorest condition. However, in the natural state most of the individuals in the summering colonies are adults and require a minimum of sustenance. In the present experiment the adults transferred to the leaves were capable of reproducing, yet most of the progeny were incapable of growing and surviving. The presence of tending ants benefits the aphids by preventing interruptions in feeding and encouraging feeding. It is well documented that ants have this "tranquillizing" effect on

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aphids (Way, 1963). The ants benefit by the continued existence of the summering aphid colonies which ensure that the ants have at least a brief period of abundant honeydew during the fall when the aphids resume reproduction on the senescing leaves. Nor would the summer tending be without immediate benefit for the ants as their honeydew requirement is greatest at this time with the maturing of the brood.

The above argument applies also, although less significantly, to *A. varians*. The observed effect of tending on survival was slight. It may be attributed simply to the prevention of "wandering" by individuals who then remained with the colony rather than leaving it.

No alatae were produced by the *A. neogillettei* colonies in the laboratory. Neither were any found in the field after July 17. A few males developed in the laboratory. As aphids used in the experiment were summering aphids, it is not unexpected that alatae were not produced. The development of the males seemed somewhat premature; however the specific timing of the production of sexuals is not known.

The proportion of apterae of the total number of surviving aphids in each colony of *A. varians* was calculated and analysed by two-way analysis of variance. A significant interaction was found ($p=.023$) and was considered important (Table 9). Examination of the treatment means revealed a significant decreasing trend (i.e., fewer apterae) in the tended colonies from densities of 10 to 100. This trend was not found in the untended colonies. The comparisons between

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Table 9. *Aphis varians*: The percent of the surviving aphids that were apterous.

Density	Tended	Untended
10	92[2]*	42[1]
50	69[12]	53[1]
100	46[1]	47[1]

*Values superscripted by the same number are not statistically different. Differences between treatment means were determined by Scheffe mutliple contrast procedures.

Anova Table Source	SS	df	MS	F	probability
Tending	.2901	1	.2901	9.65	.005
Density	.2645	2	.1323	4.40	.024
Interaction	.2652	2	.1326	4.41	.023
Error	.7212	24	.0300		
Total	1.5410	29			

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tended and untended colonies only demonstrated a difference at density 10 with more apterae in the tended colonies.

The extensive early literature on polymorphism in aphids was thoroughly reviewed by Bonnemaison (1951), Hille Ris Lambers (1966) and Lees (1966). Much of this research is difficult to assess as early researchers attributed alatae production to nutrition or some host plant factor. The role of behavioral interactions between individual aphids was not assessed. Bonnemaison (1951) demonstrated unequivocably in *Myzus persicae* (Sulzer) and *Brevicoryne brassicae* (L.) that crowding ("effete de groupe") increased the production of alatae independent of nutritional status. This was followed by detailed work by Lees (1963, 1966, 1967), on *Megoura viciae* Buckton, and Johnson (1965), on *Aphis craccivora* Koch, that showed tactile stimulation was responsible for alatae production. Since then the crowding response has been demonstrated for other aphid species (Toba et al, 1967; Sutherland, 1969a; Shaw, 1970; Dewar, 1975; Judge and Schaefers, 1971).

Johnson (1966a) found pre- and post-natal effects of nutritive status on wing formation in *A. craccivora*. This was followed by work on *Acyrthosiphon pisum* Harris (Sutherland, 1969b) that demonstrated sensitivity to host plant status with regard to wing formation. Mittler and Dadd (1962) developed a synthetic diet for raising *M. persicae*. Using a synthetic diet Sutherland and Mittler (1971) found pre-natal and post-natal crowding influenced wing formation

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in *M. persicae*.

The use of artificial diets has produced information suggesting an extremely complex relationship between nutrition, ecological factors and alary dimorphism (Harrewijn, 1978; Lees, 1966; Mittler and Dadd, 1966; Dadd, 1968; Mittler and Kleinjan, 1970; Mittler and Sutherland, 1969; Raccah et al, 1971; Judge and Schaefers, 1971; Leckstein and Llewellyn, 1973). The most significant conclusion to be drawn from the literature is that nutritional conditions affecting morph determination are not necessarily correlated with conditions that determine growth and fecundity. However, the behavioral effects resulting from those conditions affecting growth and fecundity (e.g., increased tactile stimulation from greater densities) do influence morph determination. Briefly, host plants contain substances that affect wing formation either directly or in a concentration dependent manner. For example, lithium significantly increases the proportion of apterous offspring in *M. persicae* (Harrewijn, 1976), but the effects of methionine depend on its concentration. Low levels of methionine induced restlessness in *M. persicae* resulting in more aphid-aphid contacts, producing more alatae, but higher levels do not affect restlessness (Harrewijn, 1976). These substances may be naturally present or induced by the aphid infestation.

El-Ziady and Kennedy (1956) in an experiment with *L. niger* and *A. fabae* demonstrated the ability of the ants to

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reduce alatae formation despite crowding pressures. This was confirmed by Johnson (1959) with *A. craccivora* and *Paratrachina (Nylanderia) baveri* Mayr.

Other factors influencing alary dimorphism are temperature (White, 1946; Johnson and Birks, 1960; Bonnemaison, 1951; Johnson, 1966b; White and Lamb, 1966), photoperiod (Bonnemaison, 1951; Johnson, 1966b) and parentage (Noda, 1960).

In the present study only ant attendence, crowding, host plant substances and maternal influences are relevant. Addicott (pers. comm.) has not found high alatae production at densities as low as 10 in the field. As the adults that produced the aphids that were used in the experiment came from fairly dense stock colonies, it is possible that the pre-natal crowding resulted in the production of the large number of alatae. It has already been shown that the potted fireweed were comparatively small plants and the implication of poorer nutritive status is strong.

Alatae production is viewed as an anticipatory reaction to impending environmental degradation with the alates dispersing to a more favorable location (Sutherland, 1969b). The response appears to be mediated by a complex of host plant-behavioral conditions, allowing a fine monitoring of the immediate potential of the environment to support good growth and reproduction. Because conditions favoring wing formation exist, however, it is not necessarily true that conditions for poor growth and reproduction exist. Not all

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alates migrate and should conditions prove favorable they may stay with the colony.

Ant tending exploits this alary dichotomy by preventing dispersion until the aphid colony has reached a maximum upper density at which a greater than expected proportion of alatae are produced (Banks, 1959). This situation extends the honeydew resource for the ants, while possibly not significantly effecting the potential of the aphids to found new colonies.

Maturation rates, total body length and feeding rate were used to examine differences in growth.

The average percentage (±S.E.) of adult *A. neogillettei* at each density was plotted (Figure 9). An interaction was obvious. The graph implies that there is no density effect on untended aphids, but tended aphids at the two lower densities reached maturity sooner than those at the highest density. Also, the tended aphids at the highest density do not appear to mature faster than the untended aphids.

The average adult body lengths (±S.E.) for *A. neogillettei* were plotted (Figure 10). An interaction was suggested. The only difference between tended and untended aphids appears at density 10 with tended aphids smaller. No density affect is suggested. These averages are calculated from samples ranging from 2 to 90. As such the data and implied conclusions must be viewed with caution.

Maturation rates for *A. varians* were compared by calculating the percentage of the total apterae which were

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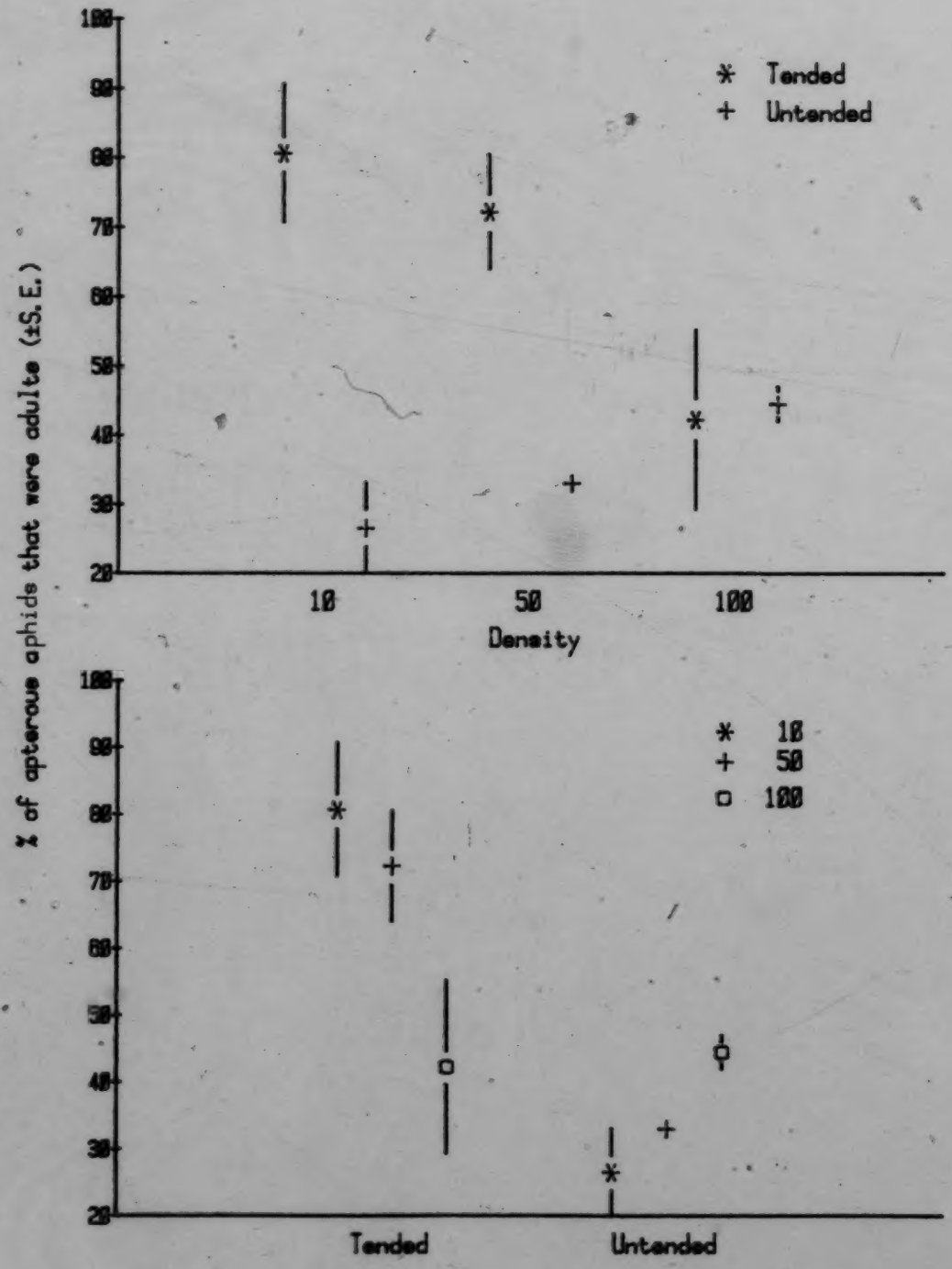

Figure 9. *Aphis neogillettei;* The percent of the apterous aphids that were adult at the end of the experment.

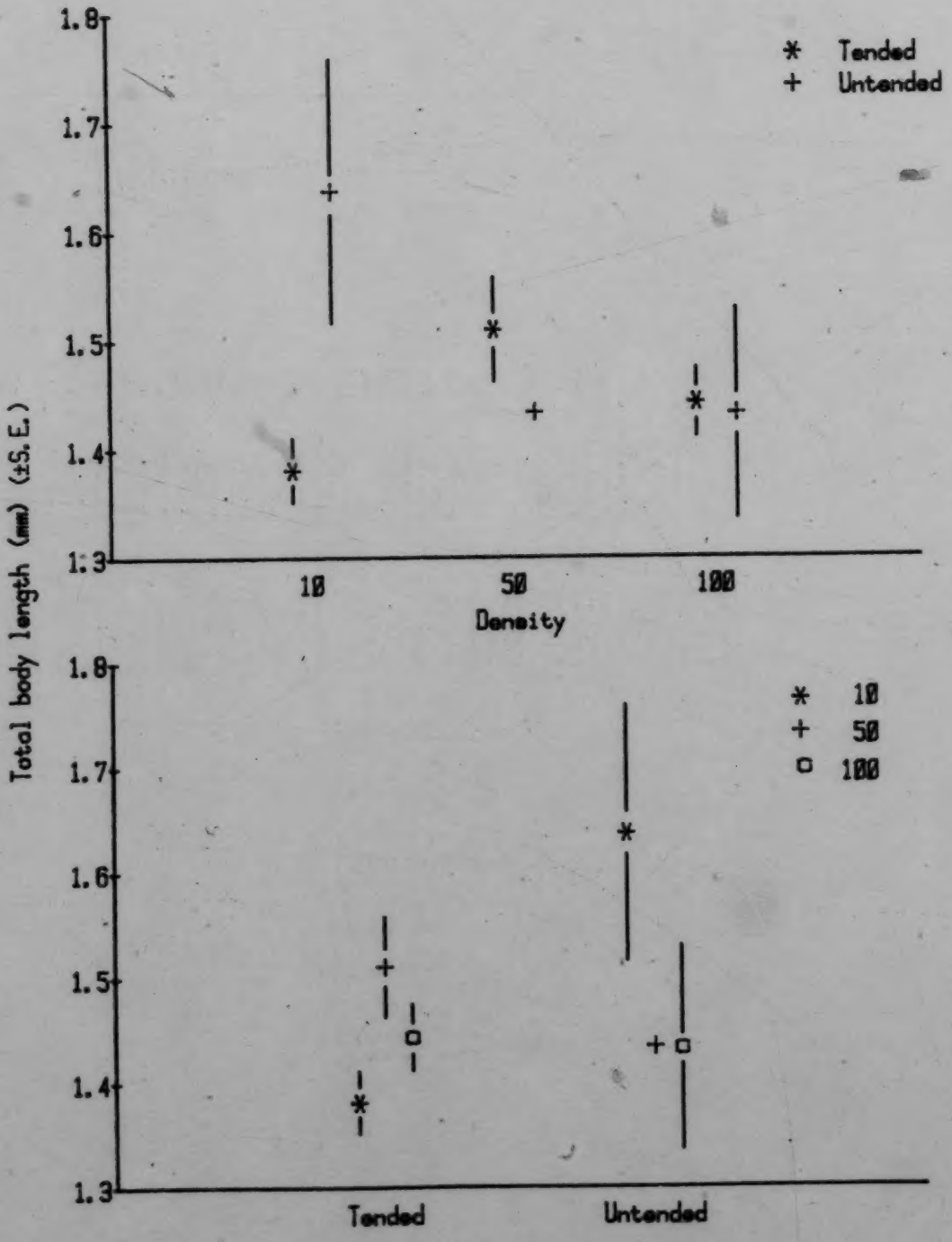

Figure 10. *Aphis neogillettei*: The average total body length (in mm) of apterous adults.

at the fourth instar and adult stage at the end of the experiment. These data were analysed by a two-way multivariate analysis of variance. Differences were examined by multiple contrast procedures analogous to the Sheffe contrasts (Morrison, 1967, pp. 182). Data on the total body length of the apterous adults were analysed by two-way analysis of variance. The alatae were excluded from the analysis as they are known to grow more slowly and reach a smaller size than the apterae (Noda, 1960). Data from density 10 colonies were also excluded from the length analysis as 4 of the 5 untended colonies had fewer than 3 adults. Time between excretions was considered as an indication of feeding rate for tended and untended aphids.

The multivariate analysis of variance on maturation rates for *A. varians* detected no significant interaction ($p=.47$) or density effects ($p=.125$, Table 10). The tending factor was significant ($p<.001$) with more adults and fewer fourth instar larvae in the tended colonies.

The analysis of total body length for the adult apterous *A. varians* demonstrated no interaction ($p=.679$) or density effects ($p=.605$, Table 11). A significant tending effect was found ($p=.004$) with tended aphids larger than untended. The average for the tended density 10 colonies was considered a good estimate as it is an average of 36 values. The data indicate that at a density of 10 the tended apterous aphids grew to the same size as the untended 50 and 100 density aphids.

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Table 10. *Aphis varians*: The percent of the surviving apterous aphids that were adult or fourth instar at the end of the experiment. (Data 2 arcsin p transformed for analysis.)

Density	Tended		Untended		Average	
	Fourth	Adult	Fourth	Adult	Fourth	Adult
10	9.9	90.1	17.5	69.2	13.4[1]	80.8[1]
50	9.6	83.5	57.6	23.4	30.8[1]	54.3[1]
100	23.7	74.6	42.0	44.9	32.5[1]	60.3[1]
Average	13.8[1]*	83.2[2]	38.2[2]	45.6[1]		

*Values superscripted by the same number are not statistically different. Differences were determined by a method analogous to the Scheffe multiple contrast procedure. Comparisons are made within an instar category and within the same rows and the same columns.

Manova Table

Source	Liklihood Ratio Test Statistic	Parameters	Probability
Tending	.517	2 23 1	<.001
Density	.726	2 23 2	.125
Interaction	.854	2 23 2	.470

Variance-Covariance Matrix

6.641	-4.596
-4.596	5.376

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Table 11. *Aphis varians*: The average total body length (in mm) of apterous adults. (Density 10 excluded from the analysis - see text.)

Density	Tended	Untended	Average
10	(1.4775)	(1.5613)	(1.5194)
50	1.6341	1.4489	1.5415[1]
100	1.6393	1.4961	1.5677[1]
Average	1.6367[1]*+	1.4725[2]	

*Values superscripted by the same number are not statistically different within the same row and within the same column.
+Differences in factor level means were determined by the Scheffe multiple contrast procedure.

Anova Table

Source	SS	df	MS	F	probability
Tending	.1348	1	.1348	10.927	.004
Density	.0034	1	.0034	.278	.605
Interaction	.0021	1	.0021	.177	.679
Error	.1974	16	.0123		
Total	.3377	19			

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The time between excretions was 15±4.7 min (n=29) for tended *A. neogillettei* and 99±11.1 min (n=24) for untended aphids. These times are significantly different (Wilcoxon T=8.43, p<.001). Tended *A. varians* excreted on an average every 10±4.8 min (n=37). Untended aphids excreted every 125±18.0 min (n=20) (Wilcoxon T=5.85, p<.001). A two-way analysis of variance (species vs tending) could not be conducted as the data were not homoscedastic. T-tests were done on the data to test for differences between species. Tended *A. varians* excrete more frequently than tended *A. neogillettei*. (t=5.45, 64 df, p<.001). The opposite is true for untended (t=5.58, 42 df, p<.001).

The average reproduction for each colony was calculated by averaging the number of embryos per adult apterae and adding that number to the average number of progeny already produced (i.e., number of first and second instar larvae divided by number of adults). The density 10 colonies of *A. varians* were excluded from the analysis because of the few adults in the untended colonies.

The average reproduction (±S.E.) for the *A. neogillettei* colonies were plotted (Figure 11). The data give no indication of differences.

No significant interactions (p=.748) were found in the data for *A. varians* (Table 12). Significant tending (p=.046) and density (p=.049) effects were found. Reproduction increased with density and with tending. As for total body length, the density 10 average for tended aphids is probably

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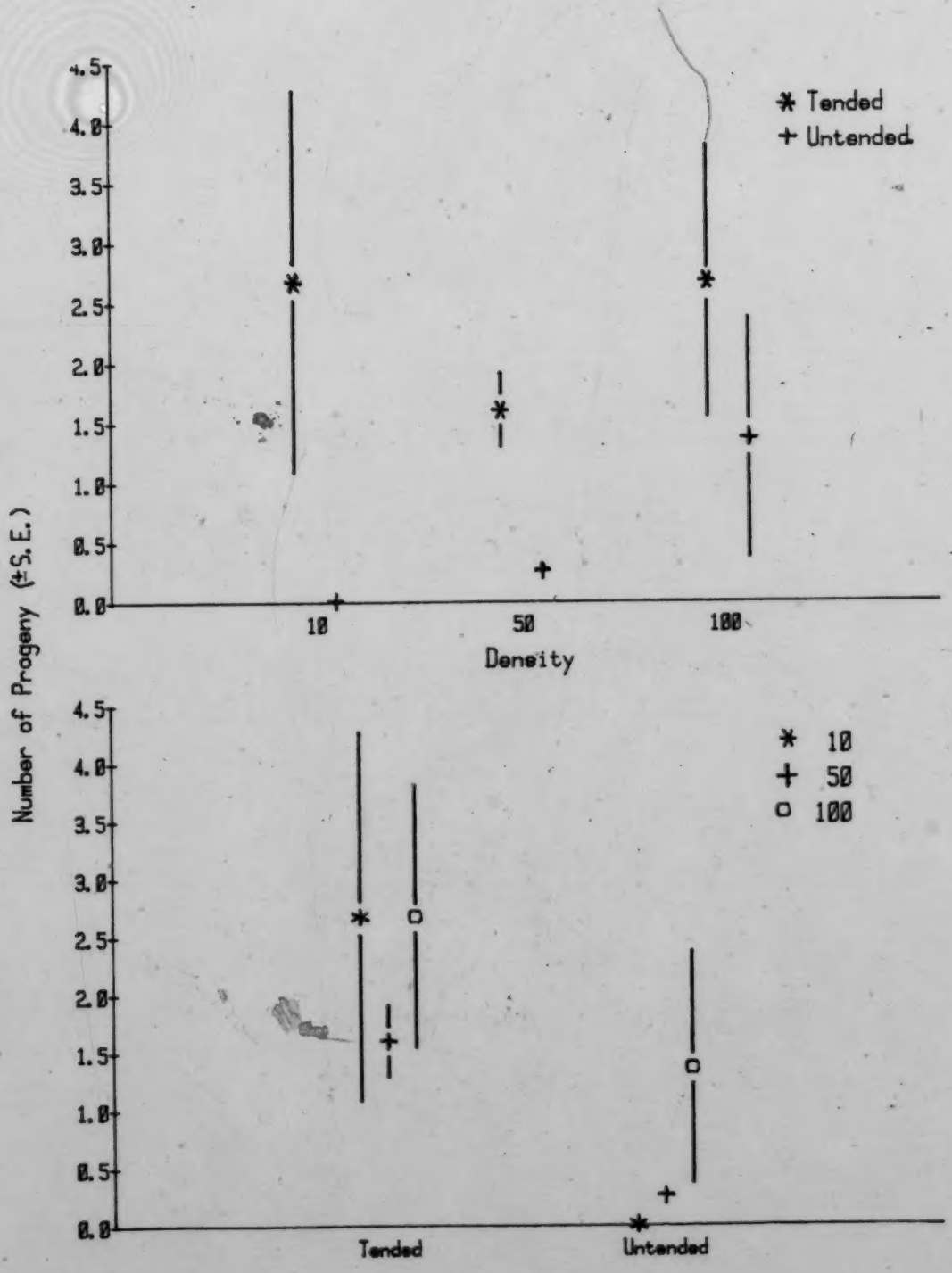

Figure 11. *Aphis neogillettei*: The average potential reproduction (average number of embryos/adult + average number of progeny/adult).

Table 12. *Aphis varians*: The average potential reproduction of adult apterae (average number of exules per adult plus average number of embryos per adult). (Density 10 excluded from analysis - see text.)

Density	Tended	Untended	Average
10	(7.50)	(5.53)	(6.52)
50	10.34	6.48	8.41[1]
100	13.13	10.28	11.71[2]
Average	11.74[1]*+	8.38[2]	

*Values superscripted by the same number are not statistically different within the same row or within the same column.
+Differences between factor level means were determined by the Scheffe multiple contrast procedure.

Anova Table

Source	SS	df	MS	F	probability
Tending	56.247	1	56.247	4.678	.046
Density	54.516	1	54.516	4.534	.049
Interaction	1.280	1	1.280	.106	.748
Error	192.394	16	12.025		
Total	304.437	19			

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a valid estimate. The reproduction at density 10 was lower than at the higher densities.

The data on the average length of first instar *A. varians* were analysed. No significant interaction (p=.73) or density (p=.82) effects were found (Table 13). However, the tending factor was significant (p=.039) with the progeny of tended aphids larger than those of untended.

Generally, tending by ants increased the rate of maturation, size, reproduction and rate of feeding for at least *A. varians*. The only effect of increased density was increased reproduction, although for tended aphids only, there is an indication that size also increased with density.

The literature states that aphid populations appear to flourish when tended by ants (Way, 1963; Nixon, 1951). Herzig (1937 - cited in Way, 1963) was the first to state quantitatively that *L. niger* caused populations of aphids to multiply two to three times as fast, and stimulated their intake of sap. He implied that better nutrition from increased feeding was the benefit from tending, dismissing protection from predators and better "hygiene" as major contributions. Banks and Nixon (1958) confirmed that *A. fabae* did excrete greater quantities of honeydew when tended. This was followed by work by Banks (1959) that demonstrated increased aphid numbers in ant-tended populations. He attributed the increase to better nutrition brought about by the retardation of dispersal from the

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Table 13. Aphis varians: The average total body lenghts of first instar larvae (in mm).

Density	Tended	Untended	Average
10	.6347	.6198	.6272[1]
50	.6369	.6080	.6225[1]
100	.6515	.6125	.6320[1]
Average	.6410[1]*+	.6134[2]	

*Values superscripted by the same number are not statistically different within the same row or within the same column.
+Differences between factor level means were determined by the Scheffe multiple contrast procedure.

Anova Table

Source	SS	df	MS	F	probability
Tending	.00527	1	.00527	4.841	.039
Density	.00043	2	.00022	.196	.820
Interaction	.00069	2	.00034	.316	.730
Error	.02396	22	.00109		
Total	.03035	27			

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apical growing points caused by tending. He also showed that ant tending of larval aphids did not affect their reproduction as adults. This last experiment, however, did not demonstrate the effects of concurrent ant tending on the adults. Nor did it examine the reproductive rate over the period of the experiment. Only total reproduction was examined.

El-Ziady and Kennedy (1956) found L. niger increased the rate of multiplication of *A. fabae* populations whether or not predators were present. El-Ziady (1960) conducted thorough experiments over 5 generations of ant-tended and ant-free aphids. She found maturation rate, growth rate and larviposition rates to be faster for tended aphids. Ant tended aphids were larger. Once adults that were tended produced large numbers of progeny, they were more apt to wander than untended aphids.

All the above parameters - alatedness, maturation rate, size and reproduction are physiologically related. For example, in aphids studied to date reproductive rate was fastest at the beginning of the reproductive period (Taylor, 1978; Dixon and Wratten, 1971). Reproductive rate was size related with smaller aphids having a longer pre-reproductive period after the teneral moult and producing at a slower rate. Longevity was related to size with small aphids not surviving to post-reproductive period. Thus, realized fecundity must be viewed as a result of a complex of interactions affecting size.

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These physiological parameters have been shown to be under the influence of juvenile hormone in many insects. Recent work by Kleinjan and Mittler (1975) has isolated a juvenile hormone analogue in the mandibular glands of *F. fusca*. When this chemical was extracted and applied topically to first instar larvae of *A. fabae*, the number of apterae increased.

Wigglesworth (1936,1948) first isolated juvenile hormone (JH) and determined its effects to be a suppression of metamorphosis accompanied by increased growth. The increased growth is the result of increased mitotic activity in the larval parts. Higher titres of JH result in a shift from gradient to isometric growth and accelerated moulting (Novak, 1975). Wigglesworth (1936) also determined JH to be essential in the development of eggs past the stage at which follicular activity begins.

Since then a substantial amount of research has been conducted on JH and the endocrine glands that produce and secrete it, the corpora allata (CA). The evidence points to sustained, but not necessarily constant CA activity throughout larval life with allatectomy leading to precocious metamorphosis. The typical cycle of CA activity, except in insects that diapause as mature larvae, is the CA are turned off late in larval life and when adult development is complete, they are turned on again (Williams, 1976). It is believed that the CA are under the control of the brain through nervous connections to the corpora

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cardiaca-corpora allata complexes (Scharrer, 1957). This complex contains both ordinary and neurosecretory axons so that in theory, the control may be nerve impulses and/or neurosecretions. It is also conceivable that the CA may be controlled as well by blood-born factors arising in other areas of the body (e.g. JH substrate precursors)(Williams, 1976). Most attention has been focused on the role of the CA in adult insects with respect to reproductive cycles, yolk deposition and adult diapause. Fewer studies have been conducted on the role of the CA in larval insects.

The general pattern of JH functioning as a morphogenetic hormone during larval life and as a gonadotropin in the adult does not hold for the aphids. Ovarian growth is initiated during embryogenesis, continues throughout larval life and reaches maximum development shortly after the adult moult in apterae and 1-2 days later in the alatae (Uichanco, 1924 - cited by Elliott and MacDonald, 1976; Elliott and MacDonald, 1976 for *Macrosiphum tanaceti* and *A. craccivora*). Thus, JH functions in both roles simultaneously in aphids. Further, Leckstein (1976) has demonstrated that the CA of adult *M. viciae* is inactive.

Of interest to this study is the effect of increased JH titres on first and second instar larvae, and on adult virginoparae.

It is generally agreed that aphids begin life as presumptive alatae (Johnson and Birks, 1960). From the embryonic to second instar moult the aphid may be

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irrevocably diverted from this path, the exact critical period varying with the species. The diversion toward apterism is a neotonic development under the control of JH (White, 1968a; Johnson, 1959; White and Lamb, 1968; Kleinjan and Mittler, 1975; Lees, 1963, 1966).

The pathway by which photoperiod controls sexual morph determination has recently been elucidated (Steel and Lees, 1977; Steel, 1977, 1978). Light acting more or less directly on the paired Group I neurosecretory cells of the protocerebrum produce compounds showing serotonergic activity. These compounds result in the production, axonal transport and release of virginoparin near the ovaries. Virginoparin affects the NSC of the late embryos causing differentiation of virginoparae. If the Group I NSC are lesioned only oviparae are produced and the PAF staining axonal material is rapidly depleted. Such a pathway allows "programming" of the embryonic endocrine system without interference to the maternal endocrine system.

Alary polymorphism has been shown to be influenced prenatally and postnatally by environmental stimuli such as crowding, nutrition, photoperiod and temperature (Lees, 1967). White (1965, 1968b, 1969) proposed that prenatal morph determination was under the control of the maternal CA. However, Leckstein (1976) has demonstrated for *M. viciae* that the CA is inactive in the adult. For other insect species it has been shown that exogenous JH interferes with normal embryogenesis in a dose-age dependent manner (Injeyan

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et al, 1979; Smith and Arking, 1975; Hunt and Shapiro, 1973; Novak, 1969; Riddiford and Williams, 1967; Sehnal, 1976; Enslee and Riddiford, 1977; Tobe and Pratt, 1975). This would support the hypothesis that all maternal influences are integrated by one neural centre which then uses "directed-delivery" (Scharrer, 1972) to program the embryos brains, rather then directly affecting the embryos physiology by its own blood-born hormones. This places the control of the differentiation process in the embryo under its own CA.

JH has feedback effect on brain centres, especially in terms of prothoracopotrophic hormone secretion. It is not inconceivable that exogenous applications of JH and JH analogues affect the maternal brain centers and through them the embryonic brain, and under natural conditions endogenous JH is not secreted by the adult. There is considerable contradiction as to whether or not adult CA's are functional. The support for an active CA is based on volume changes in the CA. Leckstein (1976) cites cases of bioassay that demonstrate CA size is not related to JH secretion. His study used ultrastructure parameters as well as CA size and found the CA to be inactive. Leckstein's arguments are quite persuasive, but it remains for research to determine, preferably through bioassay, if JH is secreted, and if so, if it is secreted differentially in adult apterae and alatae producers.

The role of JH in the development of postnatal larvae

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is somewhat clearer. In numerous studies the exogenous application of JH or JH analogue on aphids that can be affected neonatally by extrinsic factors increased apterae production, caused greater growth, and greater fecundity (White, 1968b; White and Lamb, 1968; Elliott, 1975; Mackauer et al., 1979; Lees, 1967; Kuhr and Cleere, 1973; Cloutier and Perron, 1975). It is best summarized by Elliott (1975): "The higher corpus allatum activity in apterae during the larval stage promotes faster ovarian growth and preserves the juvenile (apterous) form, while in alatae, the development of wing buds and reduced ovarian growth are both coincident with a lower corpus allatum activity."

As stated previously, several explanations have been put forward to explain the "apterizing" effect of ant tending. Herzig (cited in Way, 1963) suggested improved nutrition resulting from stimulation of feeding. Banks (1959), Banks and Nixon (1958), Kennedy and El-Ziady (1956) and El-Ziady (1960) confirmed that ants (*L. niger*) conferred direct benefits on aphids (*A. fabae*). Each had a different explanation for the mechanism, but were all agreed that enhanced nutrition was the basis of the ant effect. Way (1963), in his extensive review, apparently concurred, offering further elucidation. Small aphid aggregations appeared to benefit aphids in a manner similar to ant tending. At low densities the aphids appeared to have a "tranquillizing" effect on each other until densities causing intra-specific competition were reached. It has

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since been shown that these aggregations induce metabolic changes in the host plant resulting in better nutrition for the aphids at the site of feeding (Dixon and Wratten, 1971).

High population densities (crowding) result in greater tactile stimulation between individuals, and considerable change to physiological status of the host plant (Lees, 1967; Harrewijn, 1978). These result in the production of smaller, less fecund aphids and an increase in the number of alatae. The ecological strategy is obvious - as the environment deteriorates, produce migrants to find a more suitable one. Variations include producing migrants while the environment is still optimum that have the option of staying or reacting to a sudden change by migrating. Size plasticity is also required. Reproduction in many insects has been shown to be directly related to size (Golightly, 1940; Woodroffe, 1951; Atwal, 1955; Takahashi, 1956). Aphids, however, demonstrate a wide range in size, all capable of reproducing, albeit, reproduction declines with declining size.

Aphids are a diverse and large group. They have evolved a close and successful parasitic relationship with plants. It should not be surprising or untenable to conclude that aphids are capable of monitoring, integrating and responding to their environment with fine precision. The process requires neural/hormonal control (i.e., the integration of a number of external inputs resulting in the appropriate response, which is essentially a "growth" response

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("alatedness" vs "apterousness")). What better way to externally mitigate the effects of a deteriorating, or enhance those of an optimum, environment than by hormonal control. *Formica fusca* has been shown to have this ability (Kleinjan and Mittler, 1975). A JH analogue is present in their saliva. Ants can not affect the host plant status. They can, however, affect the hormonal response of the aphids to that status both directly by applying the analogue topically and indirectly by mediating behavioral activity ("tranquillizing" affect, retarding dispersal). The immediate benefit to the ants is clear - an increase in honeydew. The apparent contradiction is the ultimate demise of an "overpopulated" aphid colony, resulting in a loss of a food source. However, it has not been shown that the deterring of alate production does in fact reduce the success of the colony in reproducing itself elsewhere. Indeed, the literature suggests that once some maximum threshold is reached, more than the normal number of alatae are produced (Banks, 1959).

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4.3.5 Other effects of ant tending

During the present experiment attendance did not significantly affect the disperion of aphids on the host plant. Because all colonies were relatively small and short-lived, these data do not demonstrate that ants do not maintain individuals in closer configuration. Banks (1959) suggested that the major effect of *L. niger* on *A. fabae* was

to keep the aphids from dispersing from the growing shoot terminal to the leaves, thus maintaining a higher plane of nutrition which results in increased growth and reproduction. As *A. varians* does not naturally disperse from the inflorescences, if this effect occurred it would be of minimal impact. *Aphis neogillettei* does move from the inflorescences, but in the field this movement was not prevented by the ants. Anecdotally, field colonies seem more tightly packed when tended (Addicott, pers. comm.).

Untended *A. varians* colonies were visibly contaminated by their own honeydew after 8 days. This occurred regularly in the stock cultures and was remedied by washing the colony under a gentle stream of water. It is probable that rain accomplishes the same results under natural conditions, thus making this a minimally important function. *Aphis neogillettei* colonies on the other hand would not be "cleaned" by rain as they occur in tightly curled leaves. Untended field colonies could often be located by a heavy growth of sooty mould on the dogwood shrub. Tended colonies rarely were infected with sooty mould. It is unknown how or if the fungi affect the survival of the aphids.

Pontin (1958) cites cases of ant aggression towards the aphids they are tending. Way (1954) found that the ant *Oecophylla longinoda* cropped "excess" scale insects (*Saissetis zanzabarensis* Williams) for food. In the present study a tending ant was observed to eat an exule as it was being born. The ant had palpated the adult aphid as it would

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for a honeydew droplet. It is highly likely that the ant was expecting honeydew or the exule was contaminated by honeydew, and this lead to the ant's behavior. No other evidence of ant predation was observed. In all situations the ants did not have an excess supply of honeydew, so such behavior would not be expected.

4.3.6 The nature of the mutualism and the potential for competition

Ants have been shown to benefit aphids in several ways. The present study has demonstrated the following effects of tending by *F. fusca* on *A. varians* and *A. neogillettei*:

1. protection from predation and parasitism
2. physiological changes
   a. inhibition of wing formation
   b. increased size and fecundity
   c. faster maturation rate
3. better "sanitation".

Two other effects of tending by ants cited in the literature (Way, 1963; Nixon, 1951) but not demonstrated by this study are:

1. prevention of dispersal
2. cropping of "excess" individuals.

The aphids provide a high quality, continuous source of food (honeydew) for the ants. Comprehensive general reviews of the food of ants and their feeding behavior can be found in Sudd (1967), Wilson (1971) and Stadling (1978). It may be

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concluded from these reviews that the composition of the food items consumed by an ant population is directly related to the population structure. The worker population is a consumer primarily of carbohydrates, while the sexual and larval forms require a mainly protein diet. The adult ant is dependent to a large extent on soluble proteins and amino acids (Abbott, 1978). The larvae are known to give up a fluid rich in amino acids and proteins, which is readily accepted by the workers (Abbott, 1978). Ayre (1967) has demonstrated that the only digestive enzyme of quantity in the digestive tract of *F. fusca* is a midgut endopeptidase. This suggests that *F. fusca* may be entirely dependent on plant exudates and honeydew for protein in the absence of brood. Therefore, the types of food items foraged upon by ants is dependent on the state of the brood as well as other extrinsic factors (such as availability of food items, temperature and season).

The mutualistic relationship between *F. fusca/A. varians* and *F. fusca/A. neogillettei* is facultative (i.e., individuals of each species can survive and reproduce in the absence of the other species). The magnitude, duration and timing of resource expenditures by members of one species will depend on the cost for such resource expenditure at that time in relation to the benefits derived (Tilman, 1978). To understand the dynamics of the mutualistic relationship, it is necessary to know what proportion of the metabolic requirements of the tending ant population is

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fulfilled by honeydew consumption (related to seasonal variation in nutrient needs), if and when this food source is critical, and how ant tending patterns relate to the critical periods in the aphid population development.

The nutrient requirements of an ant population are determined by at least one major parameter: the presence/absence of brood. Less energy is required to sustain an adult population, and it would be primarily carbohydrate in nature. Healthy adult populations have been successfully maintained on diets that mainly consist of carbohydrates (Lamb, 1959). When brood is being raised, foragers must strike a compromise between adequate carbohydrate and adequate protein intake. Plant sap and exudates particularly from woody plants are the first available food sources for ants in early spring. There is some indication from the literature that the early production of extrafloral nectaries by some woody plants is an enticement for ants who rid the plants of insect defoliators (Tilman, 1978). The earliest aphid colonies appear on the developing inflorescences and leaves where ants are foraging for sap and nectar. By late spring the woody plants no longer provide food (in the form of nectar) for the ants, but the aphids feeding on those plants provide honeydew. Ayre (1959) stated that *F. subnitens* switched from feeding on plant exudates to honeydew as soon as aphids became available. Ayre also claimed that the ants collected more honeydew in late summer than in the spring. I

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hypothesize that honeydew collection will increase from spring to fall, but will be held in check by the need for protein by the developing brood until mid to late summer.

The two aphids studied during the present research characterize the two main life cycle strategies of aphids in general. Aphid species that occur on one host plant for their entire life cycle (usually woody plants) face a period of nutrient stress following the active growing season of the host (e.g., *A. neogillettei*). The strategies used to overcome this stress range from the production of the sexuals before this period to "aestivation" until more favorable conditions occur in the fall (senescing of the leaves). Other species avoid the stress entirely by migrating to host plants that are still growing (herbaceous plants)(e.g., *A. varians*). This situation presents ants with a choice of large established aphid colonies (on woody plants) that are beginning to decline reproductively, and many new, small aphid colonies on herbaceous plants. These small colonies experience rapid growth and have the potential to reach large population sizes, although few actually do. These dioecious aphids must compromise between establishing few large colonies (by producing mostly apterae), which are subject to extinction by predation if found by predators, and establishing many small colonies (by producing a large proportion of alatae at comparatively lower population densities). The ants must select a strategy that allows them to collect sufficient honeydew without

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undue expenditure of energy searching for new aphid colonies.

I hypothesize that competition for tending ants between aphid species that demonstrate different life history stategies would occur at the time of the summer migration of the dioecious species. At this time the monoecious aphids are still abundant and represent less of an energy expenditure to the ants. As the summer progresses ants that continue to tend the aphids on woody plants are faced with a decreasing honeydew supply as the aphids decline in numbers. The aphids require continued protection from disturbance over this time and should make themselves more "desireable" to the tending ants. Analysis of the data on the number of ants tending both species showed that more ants tended *A. neogillettei* than tended *A. varians* ($p<.001$, Table 14). This was confirmed observationally as no *A. neogillettei* colony was ever untended, even when only 1 or 2 individuals remained. This was not true for *A. varians* where 3 colonies at density 10 were tended for only 48%, 50% and 81% of the time respectively. This evidence is superficial in that a given amount of tending may have more or less benefit for a given aphid species. If the honeydew requirement of the ants increases over the summer, and more foragers are released from collecting protein food items for the brood, more ants will be available to tend aphid colonies on herbaceous plants. Also as the summer progresses more adult ants are available as the brood matures. Hence, competition should

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Table 14. Average number of aphids/ant for days 2 to 6 of each experiment. (Data in transformed for analysis.)

Density	Species *A. varians*	*A. neogillettei*	Average
10	7.94	1.71	3.69^{1}
50	21.54	3.37	8.53^{1}
100	14.56	3.66	7.30^{1}
Average	13.56^{1}*+	2.76^{2}	

*Values superscripted by the same number are not statistically different within the same row or within the same column.
+Differences between factor level means were determined by the Scheffe multiple contrast procedure.

Anova Table

Source	SS	df	MS	F	probability
Tending	16.4523	1	16.4523	25.69	<.001
Density	3.1814	2	1.5907	2.48	.108
Interaction	.2683	2	.1342	.21	.813
Error	13.4483	21	.6404		
Total	33.3503	26			

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decline also over the summer. This is dependent too on whether or not the numbers of ants in the total population is sufficient to tend the total aphid population of a given area.

If the question of competition is to be examined the "benefit" must be quantitatively defined. The most appropriate parameter would be the number of eggs produced in the fall. This would probably be an impossible thing to measure. Hence, the next best thing to measure would be the survival and success of migrants in establishing new colonies, alone or in proximity to other tended, established colonies. It is not sufficient to monitor the success of individual populations. Or at least it is not sufficient until a direct relationship can be shown between the duration of a single population and its success in producing eggs through the founding of other populations over the summer.

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5. Summary

The present study examined the effects of ant tending by *F. fusca* on the aphid species *A. neogillettei* and *A. varians*. The following effects were found:

1. Increased survival of tended colonies
2. Protection from predation and parasitism
3. Physiological affects
   a. Decreased alatae production at low densities
   b. Increased growth and fecundity
   c. Increased maturation rate
4. Better "sanitation"

The potential for competition between aphid species for tending ants was discussed.

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